Ecological connectivity in braided riverscapes

A thesis

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Contents

General acknowledgement

It has been 4 years since I wrote one of these. A period of time that stretches back into dim memory, yet seems inadequate to contain events that have occurred. Theses and life have progressed, along with the passage of time. Whilst the latter is constant and inevitable, the former were more erratic and certainly not passive processes. Accordingly, I want to thank the people and organisations who have smoothed the passage of my scientific endeavors, and those other people to whom I rush home to forget all about empiricisim.

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Beyond the double doors of level five, Old Zoology, is the world at large. The infrastructure of the School of Biological Sciences, the University and the wider scientific community. Although accusations of insularity are sometimes levelled at the

latter I have always found people interested and enthusiastic, a bit busy, but in no way elitist or aloof. From 9 to 5 ish I feel very much part of a community. Travis Horton and Dave Arscott deserve particular mention for generosity with their time, insight and expertise.

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The last seven years for me have been inspired by a landscape. This land is not pristine, but neither is it an example of a place long associated with people. Whilst, few populated regions of the world have reached a balance between nature and man, New Zealand still has the capacity for rapid and dramatic change. We have the opportunity to influence this change. We are going to need all the goodwill, enthusiasm and empathy available.

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What next?

Abstract

Rivers are hierarchical networks that integrate both large and small scale processes within catchments. They are highly influenced by variation in flow and are characterised by strong longitudinal movement of materials. I conducted an extensive literature review that indicated braided rivers lie at the upper end of the river complexity gradient due to the addition of strong lateral and vertical connectivity with their floodplains. The management of these rivers requires an understanding of the connective linkages that drive complexity, however in developed regions few braided river systems remain intact. The large number of relatively pristine braided rivers in New Zealand provided a unique opportunity to study physical and biotic patterns in these large dynamic systems. Initially I examined horizontal connectivity through patterns in regional and local diversity in eleven braided rivers in the North and South islands of New Zealand. Subsequently, the next component of my thesis focused on vertical connectivity through intensive investigations of energy pathways and the recipient spring stream food-webs.

The eleven river survey included sampling of multiple reaches and habitats (main channels, side braids, spring sources, spring streams and ponds) and confirmed the importance of lateral habitats to invertebrate diversity. However, I found that large spatial scales made a greater contribution to diversity than small scales, such that major differences occurred between rivers rather than habitats. This result suggested either a role for catchment-scale factors, such as flow, or biogeographic patterning. Subsequent analysis of the relationships between invertebrate diversity and the physical environment indicated strong regulation by flow variability, but also biogeographic community patterns. Braided rivers are clearly disturbance dominated ecosystems, however the effects of disturbance are manifest in different ways across the riverscape.

The role of vertical hydrological connectivity in linking the different components of the floodplain was investigated by tracing carbon pathways from the terrestrial floodplain to spring-fed streams and their communities. Using $\delta^{13}C$ isotope signatures it was possible to show that inorganic carbon in groundwater was derived from terrestrial vegetation and subsequently incorporated into spring stream food-webs. However, the degree to which a

stream community uses groundwater as opposed to allochthonous carbon is affected by the successional stage of riparian vegetation, a function of the shifting habitat mosaic that is regulated primarily by flow variation and sediment dynamics. In summary, the structure of braided river ecosystems is regulated primarily at the catchment scale, but connectivity at smaller scales plays an important role in determining ecological structure and function.

General Introduction

Braided rivers were once a dramatic component of landscapes around the globe (Tockner et al. 2003). However, in many areas of the world anthropogenic modification of catchments and rivers has drastically altered them (Ward & Stanford 1995; Tockner & Stanford 2002; Nilsson et al. 2005). The modification of these complex natural systems has markedly reduced the physical heterogeneity and biotic diversity of modern landscapes.

Rivers are important not only for their intrinsic values, but because they serve to integrate phenomena which occur across entire catchments and beyond. This concept was originally axiomated for modern stream ecologists by Hynes (1975) who wrote that "in every respect the valley rules the stream". In braided rivers this is particularly important because of the high connectivity between habitats found both across the floodplain and longitudinally along the riverine system. The conceptualisation of connectivity by stream ecologists has borrowed from a subset of general systems theory that deals with hierarchies (Allen & Starr 1982; Stanford & Ward 1993). Organisms, habitats, or stream reaches are nested within physical and organisational elements, which exist at a higher level within the hierarchy. In ecological systems generally, it has become apparent that linkage and regulation feedbacks propagate patterns and process up as well as down the scales of this hierarchy (Harrison & Cornell 2008). Thus, hierarchically scaled approaches are highly appropriate for rivers, which form dendritic networks and are open, "leaky" systems within an often highly heterogeneous matrix (Pringle et al. 1988; Power & Dietrich 2002; Lowe et al. 2006; Grant et al. 2007).

The role of disturbance has also emerged as a major paradigm in ecology (Connell 1978), and particularly stream ecology (Resh et al. 1988; Death & Winterbourn 1995; Townsend et al. 1997; Lake 2000). Disturbance can dictate the structure of biotic communities at both ecological and evolutionary scales (Lancaster & Belyea 1997; Diaz et al. 2008), and braided rivers probably represent the quintessential disturbance-dominated freshwater ecosystem (Scrimgeour & Winterbourn 1989; Tockner et al. 2006). However, this

description also obscures the more subtle effects flooding has on the creation of the high physical heterogeneity that defines floodplains (Arscott et al. 2002; van der Nat et al. 2003; Hauer & Lorang 2004; Latterell et al. 2006).

Our current understanding of the relationship between the physical environment and biological communities integrates hierarchy and disturbance theory. However, this approach is limited by our ability to identify important levels within the hierarchy (Kolasa 1989) and the routes by which disturbance and other linkages are transmitted between scales (Lowe et al. 2006). The key to this conundrum is an understanding of the physical and biological connectivity that regulates natural systems (Stanford & Ward 1993; Ward & Stanford 1995; Ward et al. 1999; Pringle 2001). New Zealand is fortunate to have retained a number of relatively pristine, braided, floodplain systems with which to address some of these fundamental ecological issues.

Thesis layout

This thesis is presented as a series of independent manuscripts, some of which have been published and some submitted or in preparation. Consequently several chapters share introductory material and when they have been published the publishing format has been retained.

Chapter 1 is a literature review that summarises the international and New Zealand literature on braided rivers, with an emphasis on benthic invertebrate ecology. Particular attention has been paid to the physical template of braided rivers and the implications of anthropogenic catchment modification on the physical and biological features of these systems. Chapters 2 and 3 present analyses of a survey of eleven New Zealand braided rivers. The survey had a nested, hierarchical design and included braided river systems from regions throughout the country. In each river, 6 reaches and up to 5 floodplain habitat types per reach were sampled. In chapter 2, I investigate diversity patterns within and between the nested scales of habitat, reach, river and island. In chapter 3, I have built on this analysis by focusing on the environmental drivers which shape invertebrate diversity and community composition. The research reported in both chapters 2 and 3

sought to investigate the role of horizontal connectivity between elements; dispersal and biogeographic patterns within the contemporary physical environment (Figure 1).

Figure 1. The Clyde River in Canterbury set amongst substantial dispersal barriers.

Chapters 2 and 3 highlight the importance of horizontal connectivity and lateral habitats, especially springs, to the overall structure and function of floodplain invertebrate communities. A logical extension of this work on horizontal connectivity was to investigate the influence of vertical connectivity in these particular habitats, in particular the energy flow into spring habitats. These questions are addressed in chapters 4 & 5 which track the flow of carbon from groundwater into the spring streams. In chapter 4 I used stable isotopes of dissolved inorganic carbon (DIC) and food-web components to trace the cycling of carbon between terrestrial, subterranean aquatic, and surface aquatic, floodplain components (Figure 2). Chapter 5 investigates the role of riparian vegetation and floodplain succession in influencing carbon dynamics in spring streams.

Figure 2. Abundant bryophyte and algal growth close to the source of a floodplain spring, Waimakariri valley. Photo Jens Zollhoefer.

The final synthesis draws together the main findings and implications of this research. Appendices 1 and 2 are published papers, which arose incidentally in the compilation of this thesis. Appendix 1 is the formal description of a new species of Plecoptera found in a spring creek of the Clyde River, Canterbury. Appendix 2 discuses the natural history of *Namanereis tiriteae* a rare freshwater polychaete encountered in the North Island. Appendix 3 is a presence/absence list of the taxa found in each of the eleven braided rivers considered in this study.

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Chapter 1. Braided river ecology: a literature review of physical habitats and aquatic invertebrate communities

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Abstract

Globally, braided rivers are distinctive freshwater ecosystems, characterised by highly variable flow regimes and unstable substrates. Many braided rivers have been subjected to human modification. In New Zealand, many braided rivers remain in a relatively unmodified condition, but increasing demands for hydro-electricity generation, irrigation, gravel extraction and flood protection works are placing pressure on these systems. This review summarises the international and New Zealand literature on braided gravel rivers, with particular emphasis on benthic invertebrate ecology. We define a braided river as a lotic system with multiple, mobile channels distributed across a gravel floodplain. Braided rivers typically experience short-term channel migration within the active bed and greater lateral channel migration across the entire floodplain in the longer term. Channel migration occurs because steep headwater tributaries supply highly variable discharges and mobile erodable substrates to the mainstem. Braided rivers typically possess extended floodplains, which may contain a mosaic of floodplain habitats ranging from highly unstable main-stem channels to stable spring complexes. Main channel aquatic invertebrate communities are frequently low in diversity and dominated by the leptophlebiid mayfly *Deleatidium* spp., but also chironomids and elmid beetles. In contrast, floodplain springs can have highly diverse communities rich in amphipods, mayflies, caddis, snails and chironomids. Groundwater and floodplain pond habitats also occur frequently and can contain several specialist taxa. The traditional view of braided rivers as highly disturbed, species-depauperate, 'ecological deserts' has been altered by recent studies that recognise these rivers and their floodplains as spatially complex,

temporally dynamic habitats with high landscape- and reach-scale biodiversity values. The challenge facing managers is to protect this biodiversity within the context of increasing human demands on braided rivers.

1.0 Introduction

1.1 The scope of this review

The aim of this review is to summarise the literature available on braided rivers in New Zealand and overseas, with particular emphasis on our understanding of the diversity and structure of aquatic invertebrate communities in these ecosystems. The introductory section defines braided rivers and describes the location and condition of braided rivers. The review then considers the habitat template and the physical characteristics of the floodplain habitats typically found within braided rivers, and the ecological patterns generated by this template. The biotic communities of typical floodplain habitats are presented and finally we discuss the threats, management issues and research gaps associated with braided rivers in New Zealand.

1.2 Definition of a braided river

A number of definitions have been suggested to describe braided rivers.

> "Braided rivers are characterised by having a number of alluvial channels with bars and islands between meeting and dividing again, and presenting from the air the intertwining effect of a braid." (Lane 1957).

> "A braided river is one which flows in two or more channels around alluvial islands." (Leopold and Wolman 1957).

Braided rivers have been historically described based on the physical characteristics of the river reach. Leopold and Wolman (1957) suggested that numerous channel types can be identified within rivers, including, braided, meandering and straight channels. However, multiple channel types may often be found within a single reach such that further attempts at classification of the entire reach become difficult. Reinfelds and Nanson (1993) described a "braided river floodplain" as the generally extensive, vegetated and horizontally bedded alluvial landform, sometimes composed of a mosaic of units at various stages of development, formed by the present regime of the river,

occurring within or adjacent to the un-vegetated active river bed and periodically inundated by over bank flow.

For the purpose of this review we define a braided river as a river that at some point in its length flows in multiple, mobile channels across a gravel floodplain. There must be evidence of recent channel migration within the active bed of the river and of historical movements of the active bed across the floodplain. The lateral and vertical limits of the 'river' include the entire width of the floodplain and the saturated depths of the alluvial aquifer, within and across which the river moves as a single body of water.

1.3 What conditions create braided rivers?

Leopold and Wolman (1957) proposed two primary controlling variables on channel pattern; discharge and slope, for which two rules are apparent. First, for a given discharge and bed material, there are threshold slopes between which channels will braid, and second, that the critical slope decreases with increasing discharge or decreasing sediment size. Both slope and bed material change naturally and predictably down the river. In general, catchments are steeper in their headwaters and the bed materials are coarser; however as we move downstream, slope decreases and bed materials become finer (Browne 2004). Consequently, channel form changes in a fairly predictable fashion downstream. Nevertheless, smaller-scale changes in slope and bed material, in conjunction with temporally variable changes in discharge, mean that braiding can occur irregularly along the length of the river. A period involving several high discharges may produce a distinctly braided channel pattern, whereas a period of climatic stability, over months or even years, may produce a channel pattern tending towards a single, straight channel (Bridge 1993, Whited et al. 2007).

Geomorphologists have developed indices of channel type, which consider surface physical attributes including, channel splitting and sinuosity, and the stability of floodplain bars and islands. Increasingly complex attempts at classifying channel types are summarised by Bridge (1993) and Sambrook Smith et al. (2006). However, more recently, research has highlighted the multi-dimensional nature of braided rivers and

provides a more complete understanding of the role of the river and its floodplain within the greater catchment (Stanford and Ward 1988; Brunke and Gonser 1997; Woessner 2000). We now understand that braided rivers consist of much more than active surface channels, and that the river flows across an alluvial gravel bed, which may be many meters deep and possibly kilometres wide. Surface water flows over the top of the gravel, but also moves down vertically and horizontally though the gravels as groundwater. This groundwater, which may re-emerge as a spring or wetland, is the vertically connected component of the braided river. Despite the pre-occupation with surface characteristics, braided rivers are three-dimensional ecosystems. They are a single body of water moving down the river corridor exerting an influence far beyond the "bank" of the active river, and it is this multi-dimensional structure which makes braided rivers so important as physical and aesthetic phenomena, as well as diverse and complicated ecosystems.

Morphologically rivers can be viewed as those constrained by narrow valleys and terraces, and those unconstrained and flanked by a floodplain (Schumm 2005). In order for a river to form multiple channels it requires a floodplain, either fluvially or glacially derived, that is wider than the combined widths of the mean flow wetted bed. Braided rivers also depend upon two catchment-scale conditions. First, a source of highly erodable bedrock, which forms the basis of gravel-dominated highly sinuous channels. This eroded material may be produced by several processes but, is usually the result of glacial activity, erosion of friable bedrock and active mountain building. Many braided rivers are found in areas that experience these erosional forces, notably parts of Canada, Alaska, the Himalayas and the South Island of New Zealand. Second, almost all braided rivers are associated with steep mountain ranges, which have the capacity to create their own weather. For example, the Southern Alps of New Zealand are aligned perpendicular to the prevailing westerly air flow, resulting in orographic rain, which can occur at any time of year. So, rivers that are not laterally constrained by some geographical feature and that experience a high level of sediment input may form an alluvial floodplain. Interactions between the hydrograph, sediment size and slope of the floodplain may create conditions that cause a river to form multiple sinuous channels across its

floodplain. However, periods of discharge stability or anthropogenic constriction of the floodplain may shift the channel form away from braiding towards a single channel.

1.4 Braided rivers globally and in New Zealand

Braided rivers occur globally, although most frequently in arctic and alpine regions with high precipitation and steep headwaters, but they also occur in arid and Mediterranean climates subject to torrential rain, and in some tropical regions where there are monsoonal rains (Bravard and Gilvear 1996). Whilst the headwaters of many braided rivers may remain relatively free from direct human modification, their lower reaches are frequently heavily impacted (Tockner and Stanford 2002). In fact, in most developed nations few examples of non-impacted braided floodplain systems remain (Malmqvist & Rundle 2002: Tockner & Stanford 2002).

Dynesius and Nilsson (1994) estimated that, of the 139 largest rivers in Europe, the former Soviet Union, USA and Canada, 77% were moderately to strongly affected by flow regulation. Human degradation of river systems is a worldwide phenomenon (Benke 1990; Raven et al. 1998; Muhar et al. 2000; Pringle et al. 2000; Rosenberg et al. 2000; Brunke 2002; Young et al. 2004; Nilsson et al. 2005) and flow regulation and channelisation are recognised as particularly important issues in braided floodplain systems (Brunke 2002; Hauer & Lorang 2004; Hohensinner et al. 2004; Thoms et al. 2005). In Europe, human modification of rivers is so common that the Tagliamento River, in north-eastern Italy, is regarded as the only remaining morphologically intact braided river system (Tockner et al. 2003). The majority of extant unmodified systems are concentrated in the extreme north of Alaska, Canada and Eurasia, away from centres of human development (Dynesius and Nilsson 1994), and in New Zealand in the Southern Hemisphere. Whilst many other alpine regions such as the Himalayas and Andes have rivers with braided reaches, the rivers are often severely degraded and published accounts of their ecology are scant (Garcialozano 1990; Gopal and Sah 1993; Wang et al. 2005; Habit et al. 2006).

Despite the paucity of unmodified systems to study, both Europe and North America have established centres of intensive research to investigate the function and landscape roles of floodplain systems (Stanford and Ward 1993; Ward and Stanford 1995; Tockner et al. 2003). Insights from these studies have supported a number of rehabilitation and restoration projects, particularly along central Europe's largest rivers (Hohensinner et al. 2004).

In New Zealand, numerous studies on the geomorphology of braided rivers have been published, and our physical braided river research continues to be at the cutting edge (Mosley 2001; Sambrook Smith et al. 2006). Furthermore, a considerable body of literature has been generated, initially by catchment and regional water boards and regional councils primarily as resource reports, draft management plans and water conservation/consent reports (NCCB 1983, 1986, 1991). However, apart from a limited number of studies on the ecology of individual species or reaches, little coordinated ecological research has taken place to asses the values and function of these eco-systems (Hughey et al. 1989; Sagar and Glova 1992; Reinfelds and Nanson 1993; Meridian Energy 2003; Gray 2005; but see O'Donnell and Moore 1983). Unfortunately, economic development, particularly demands for hydroelectric power generation and irrigation water are putting increasing pressure on New Zealand river systems (Young et al. 2004).

2.0 The habitat template: physical conditions within a braided river

2.1 Geomorphic and geologic template

New Zealand sits atop a geologically active, tectonic boundary resulting from the break-up of Gondwana (Kamp 1992). Approximately 80 mya the Tasman Sea began to open, separating New Zealand from what would become Australia and Antarctica. About 60 mya movement ceased and New Zealand has remained physically isolated ever since (Gibbs 2006). For the first 70 million years of this separation the climate is thought to have been warmer than at present and vegetation was similar to that now found in Australia and New Caledonia (Stevens 1981). At this stage, New Zealand comprised a series of low-lying islands, but about 8 mya the Pacific–Australian plate margin began to move again, lifting the seafloor and building the alpine regions. Subsequent mountain

building, volcanic activity, and periods of glacial growth and recession have produced our contemporary landscapes, particularly the major river valleys in the South Island alpine regions. Early Pleistocene glaciers were not restricted to present day valley systems, however it was during the Ross and Porika glaciations (1–2 mya) that the broad framework of modern watersheds developed (Pillans et al. 1992). Two major glaciations, the Waimaunga and Otira glaciations, further modified the existing valleys. The brief glacial recessions are particularly well documented in the Waimakariri and Taramakau catchments, and culminated with the end of the second Poulter Advance about 13 000 years ago (Gage 1977). Similarly in Europe, the Würm, and in North America, the Wisconsin glaciations, ended approximately 10, 000 years ago, therefore the most studied overseas braided river systems considered in this review are of comparable age to those in New Zealand (Muller and Kukla 2004; Smith 2004).

During the last 10, 000 years New Zealand's braided rivers have been sculpted by fluvial processes augmented by discrete tectonic events. For example, Reinfelds and Nanson (1993) described the three predominant mechanisms in the development of the Waimakariri River's braided river floodplain. First, riverbed abandonment by lateral migration of the active river bed (usually in the lee of tributary fans and bedrock spurs), followed by aggradation during high magnitude flood events, and finally localised riverbed incision. In fact, several authors have described braided rivers as being in a state of "dynamic stability", whereby despite a high turnover of habitat the proportions of each habitat type remain relatively constant over time (Arscott et al. 2002; Hauer and Lorang 2004; Latterell et al. 2006). However, over longer time scales (00's of years) it would probably not be accurate to state that these rivers are in a state of balance or equilibrium. For example, Korup (2004) used historical aerial photography and geomorphic, morphostratigraphic and dendrogeomorphic evidence from 250 landslides in south-western New Zealand to describe the channel-altering effects of landslides. At least 6% of landslides caused major avulsions (channel shifting) and it is likely that the characteristic instability of braided rivers is accentuated by sediment pulses (Hicks et al. 2004). The effect of these events upon terrestrial and aquatic floodplain habitats can be very dramatic. In 1967, the Gaunt Creek landslide caused the braided Waitangitoana

River on the West Coast of the South Island to alter its course, from merging with the Whataroa River to flowing into the Okarito River catchment. The lower reaches of the Waitangitoana River are now predominantly fed by groundwater as opposed to surface runoff, and after the landslide a large portion of the wetlands at the inflow of Lake Wahapo were buried under gravel. Goff and McFadgen (2002), Cullen et al. (2003) and Korup (2004) have documented evidence of several periodic seismic events that have caused river aggradation and driven vegetation destruction and channel instability throughout New Zealand.

2.2 Contemporary geology and geography

An extensive desk-top mapping exercise by Wilson (2001) identified all the river systems that exhibit braiding within New Zealand. Overall 163 river systems had braided reaches, with a total of 248 400 ha of braided river habitat occurring in 11 of New Zealand's 14 regions. Canterbury and the West Coast had the largest areas of braided river habitat with 60% and 19% of the national total, respectively. Braided rivers occur on both coasts of the South Island but were restricted primarily to the east coast of the North Island. Wilson (2001) also reported that North Island braided rivers have climatic conditions (temperature, solar radiation and humidity) similar to those in the northern South Island, and unlike those of the remaining portions of the South Island.

The majority of braided rivers in New Zealand drain lithologically unstable catchments predominantly of greywacke, mudstone or other sedimentary rocks, although some of the rivers in South Westland, such as the Landsborough and Arawata are dominated by schist and gneiss. In the North Island, highest sediment production occurs in the East Cape region, where high rainfall, natural geologic instability and accelerated erosion (due to deforestation) contribute to high sediment yields (Mosley and Duncan 1991; Hicks et al. 2004). Sediment yields in the South Island are highest on the flanks of the Southern Alps and those in some rivers have been estimated to be among the highest in the world (Griffiths 1979).

High precipitation on the flanks of the Southern Alps in the South Island, and on the Kaimanawa, Raukumara and Ruahine Ranges in the North Island contributes to the presence of braided rivers. Many of our braided rivers also have glacial sources and snow-laden upper catchments, which also add to their volatile hydrologic regimes. The hydrographs of the South Island's alpine rivers are characterised by large floods resulting from heavy rain along the Main Divide, often compounded by snow melt. In spring and early summer, floods are common. In contrast, during winter when water is locked in upper catchments as snow and ice, and in high summer and autumn when precipitation levels are low, many braided rivers experience extreme low flows. This trend is consistent across braided rivers around the world, the Tagliamento (Italy) and Flathead (Montana, U.S.A.) rivers having been similarly described as 'flashy pluvio-nival' (i.e. with flow characteristics dominated by rain and snow melt) (Tockner et al. 2003; Hauer and Lorang 2004). In Switzerland, the braided Roseg River exhibits a distinct glacial-melt flow regime, which features strong seasonal flow patterns and a marked diel flow pattern during the summer melt period. These diel patterns are generally absent in New Zealand's braided, glacial rivers as any patterns are usually masked by high rainfall during the melt season (McSaveney and Davies 1998).

2.3 Contemporary floodplain habitat

Despite the physically unstable nature and high turnover of habitats found on braided river floodplains, their biological communities survive because the relative proportions of each habitat remain roughly constant (Arscott et al. 2002; Hauer and Lorang 2004; Latterell et al. 2006). Consequently, mobile taxa may persist within the floodplain, and form part of a meta-population within the river system (Begon et al. 1996). Furthermore, the existence of habitats in different successional stages provides a highly diverse mosaic of floodplain habitats, each with its own distinct biological communities. In New Zealand, Burrows (1977) reviewed the literature on riverbed vegetation of the upper Waimakariri River basin and suggested a time scale for the successional colonisation of riverbed features. Building upon his study, and using aerial photography from 1948 to 1986, Reinfelds and Nanson (1993) proposed that the Waimakariri River re-works its entire floodplain every 250 years, predominantly by lateral migration of the most active

part of the braid (Fig. 1). Thus, floodplain habitats may be destroyed by high flows and channel movement on one side of the floodplain while new habitats are developing on the other side of the floodplain.

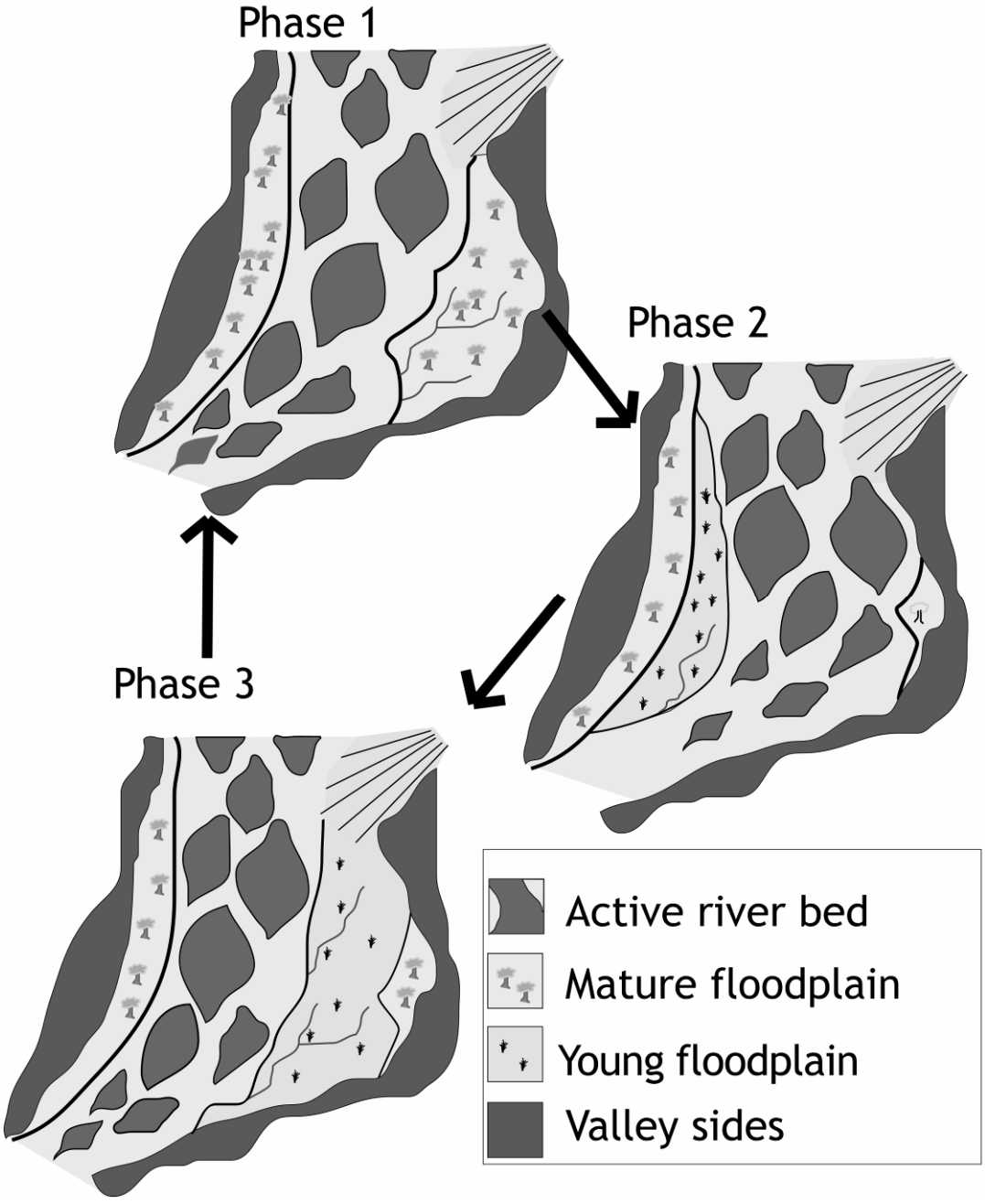


Figure 1. Floodplain re-working by lateral migration of braided channels. Adapted from Reinfelds and Nanson (1993).

A similar study by Warburton et al. (1993) in the upper Ashley River in Canterbury, observed the presence of stable bars and islands amongst the unstable materials, and noted that the active channel of the river was steadily migrating northwards. Mosley (1982a) made use of controlled water releases along the braided Ohau River to estimate the effect of varying discharge from 26.5 m^3/s to 507 m^3/s on channel morphology. As discharge increased, the physical characteristics of existing channels changed, and new channels formed that were physically similar to the original channels. Mosley concluded that across the range of discharges the habitat types available remained proportionally relatively constant, and thus braided rivers in some respect may be morphologically more stable than a single-thread river. More recent work has focussed upon riverbed turnover within the lower Waimakariri River. A combination of digital photogrametry and LiDAR (Light Detection and Ranging or Aerial Laser Scanning) have been used to create 3-D models of the river bed which may be compared over time to investigate the influence of flooding on river morphology (Hicks et al. 2003, Lane et al. 2003, Westaway et al. 2003, Hicks et al. *In Press*). Although not specifically focussed upon in-stream habitat types Hicks et al. (*In Press)* have shown that the Waimakariri River turns over 2/3 of its available floodplain annually (specifically >0.2m vertical erosion or deposition) and would probably re-work the entire floodplain within 5 years. The most persistent areas of wetted habitat were those found within the dynamic braids, and thus the most physically disturbed of the aquatic habitats available. These findings highlight the potential ecological value of spatially minor, but more stable peripheral floodplain habitats. Temporal mapping of habitat types within New Zealand braided rivers has not been done to confirm habitat dynamics and the appropriateness of the shifting mosaic steady state model, although it is considered applicable to unmodified New Zealand systems (M.D. Hicks, personal communication 2007).

The role of large woody debris in structuring stream morphology is well documented both overseas and in New Zealand (Gurnell et al. 2002, Hicks et al. 2004). In small New Zealand streams large woody debris has been shown to influence channel morphology and pool formation, as well as being an important habitat for invertebrates in streams with otherwise unstable silt or pumice substrates (Hicks et al. 2004). Whilst the role of

large woody debris has not been assessed in New Zealand's braided rivers, studies overseas indicate that wood may play an important role in large rivers (Gippel et al. 1996, Gurnell et al. 2000a, Van der Nat et al. 2003). In large rivers wood has been associated with the creation and maintenance of bars and islands and sites for avulsion and the formation of secondary channels. Pools form around embedded logs in response to flow diversion imposed by the root wad and fine sediment accumulates downstream along the trunk (Gurnell et al. 2002). Many rivers in Europe suffered major deforestation of their riparian zones prior to the 16th century, however investigations of woody debris accumulations in the semi-pristine Tagliamento River, Italy, have revealed the links between river morphology and riparian forest/woody debris. Wood storage within the active channel of the Tagliamento is spatially variable. Small quantities were found on the open gravel surfaces and intermediate quantities with mature islands, but large quantities were associated with pioneer or developing islands. The majority of this wood accumulated on bar crests, the point of formation for pioneer islands (Gurnell et al. 2000a, Gurnell et al. 2000b). Islands form in the lee of debris jams as evidenced by the decreasing age of vegetation from upstream to downstream. The process of vegetated island development may also be accelerated if the woody debris is still alive and able to sprout (Gurnell et al. 2002). Furthermore, woody debris appeared to be more abundant in headwaters than the lower reaches and thus under natural vegetation conditions a debris gradient occurs along the river. How this longitudinal gradient and the movement of wood downstream affects flow, habitat and the availability of carbon to food webs is poorly understood.

The condition and age of vegetation along the riparian corridor may substantially influence channel geomorphology, primarily by altering bank strength and flow resistance (Gran and Paola 2001). Numerous studies have linked channel properties such as width, depth and velocity to vegetation density in the riparian corridor (Graf 1978, Andrews 1984, Hey and Thorne 1986, Huang and Nanson 1997, Rowntree and Dollar 1999, Millar 2000), and between vegetation type or density and channel form, e.g. braided or meandering (Mackin 1956, Brice 1964, Nevins 1969, Goodwin 1996, Gran and Paola 2001). However, in many developed regions globally, riparian forests have

been removed to create farmland. In New Zealand, much indigenous riparian forest has been removed and replaced with tussock grassland and pasture (Miller 2002). Subsequently, thousands of kilometres of stream and river banks have been re-planted with willows in order to prevent floods from damaging adjacent farmland (Miller 2006; Mosley 2004). Mosley (2004) suggested that rivers in New Zealand maybe responding to increased riparian re-aforestation by narrowing, and for some lowland Canterbury rivers this may represent a return to the stable anastamosing form they had prior to deforestation by Maori and European colonists.

3.0 Floodplain habitats of braided rivers

3.1 Main channel and side braids

Most braided reaches will include one or more larger channels which persist between flood and drought events. Typically these larger channels will have multiple side channels which exemplify the characteristics of a braided river (Fig. 2). The flow regime of the main channels and side braids can be highly variable.

Figure 2. A typical braided river main channel in the Hopkins River.

The substrate of the main channel can be highly unstable. In the upper Waimakariri River, Gray (2005) recorded 99% movement of cobble-size tracer stones over a 6-month period. In the lower reaches of the same river Hicks et al. (*in press*) estimated that 88% of the riverbed had undergone significant (>0.2m vertical erosion or deposition) change during a 3-year period. Whilst main channels and side braids are part of a continuous surface network, they are not always subject to the same disturbance regime. Side braids may have more stable substrates, as evidenced by algal growths but, also be subject to more regular de-watering with river stage fluctuations. Furthermore, the hydrological source of the river (alpine or foothill), will influence the regularity and intensity of physical disturbance in all channels.

Main and braided channels are major conduits for sediment transport. Estimated sediment yields from New Zealand's braided rivers may be among the highest for rivers anywhere in the world and despite amounting to only 0.2% of the world's landmass New Zealand produces 1% of the sediment input to the worlds oceans (Griffiths 1979; Hicks et al. 2004).

Temperature regimes in the main channels and side braids are influenced by variations in channel discharge, and the relative contributions of groundwater and surface water runoff (Mosley 1983b). Mosley (1983a), found that during autumn and spring maximum temperatures of the main channel in the Rakaia and Ashley Rivers were inversely proportional to discharge however, Grant (1977) reported main channel temperatures in the Ngaruroro River in Hawkes Bay, were lower when the river was at base flow than at high flow owing to the increased influence of groundwater. Thus, the ground or hyporheic water may buffer the main channel against relatively warmer surface water runoff and atmospheric temperature fluctuations. Under low flow conditions water temperatures can, however become very high in the absence of groundwater exfiltration, and in mid-summer temperatures in excess of 25^{o}C have been recorded in Canterbury rivers (Mosley 1982b).

3.2 Springs

Springs can be common in braided river floodplains but constitute a small proportion of the wetted surface area of a braided river. The roles of springs within the braided river landscape are discussed in this review, and put into the greater context of other spring types, e.g. Karst springs, nationally within (Scarsbrook et al. 2007). Springs have distinct physical and chemical characteristics (Fig. 3) compared to the main channels (cf. Fig. 2) and see (Fig 7).

Figure 3. A floodplain spring in the Hawdon River, Arthur's Pass National Park. Note the abundant macrophytes and mosses.

Braided river springs derive their flow from aquifers and therefore although some springs are very stable and permanently wet, others may be subject to drying. Spring permanence appears to be linked to the position of the spring in relation to the main channel and the height of the spring relative to the water table of the floodplain (Poole et al. 2002, Poole et al. 2004). Spring discharge is characteristically stable (Fig. 4) and frequently reflects the broad-scale trends in discharge of the main river, but without the

dramatic peak flows characteristic of surface runoff-fed streams (Death 1991; Barquin 2004; Gray 2005).

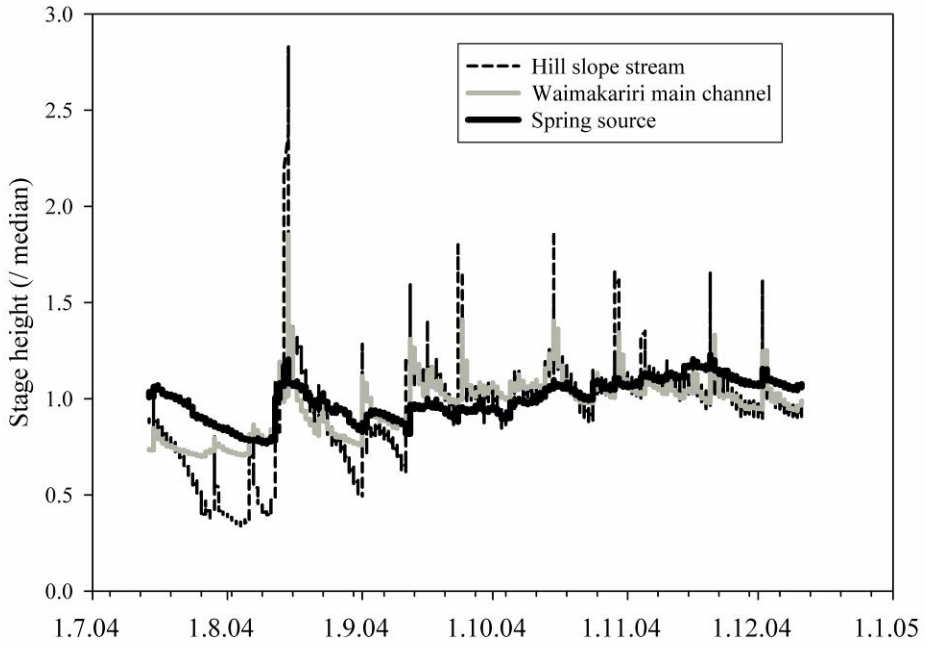


Figure 4. Stage height (standardised to the median value) of a hillslope stream, a spring-source and the main channel of the Waimakariri River (Gray 2005).

Consequently, the substrate within spring-fed streams is usually very stable and the water clarity high. Gray (2005) estimated the percentage of substrate movement in floodplain springs in the Waimakariri River to range from 2 - 12% per annum. Similarly, Death (1991) detected no substrate movement over 2½ years in Slip Spring, also in the Waimakariri River basin. The substrate composition of spring creeks is frequently a result of historic deposition and occasional flooding from adjacent surface-fed streams and rivers, rather than in-stream processes. Overbank flooding tends to introduce fine sediment to the spring, and may be augmented by aeolian (windblown) deposits (Reinfelds and Nanson 1993).

Temperature regimes of floodplain streams in New Zealand that are spring-fed are more stable than those of main channels and approximate the local mean annual air temperature (Death 1991; Gray 2005) (Fig. 5). Thus, spring creeks tend to be warm in winter and cool in summer compared to surface-fed streams (Mosley 1983b). However, temperature fluctuations increase with distance from the point of up-welling (Barquin 2004).

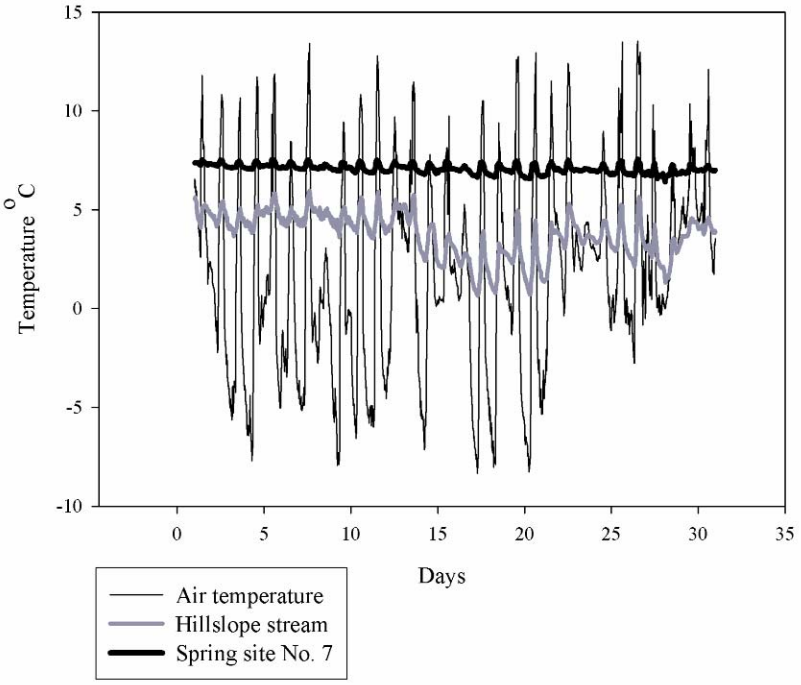


Figure 5. Temperature regimes for air temperature, a spring-fed and a surface runoff stream between the 15th July and 13th August 2004, (Gray 2005).

3.3 Groundwater and hyporheic zones

Groundwater's beneath a braided river are generally sub-divided into two inter-grading zones; the hyporheic and phreatic zones. The hyporheic zone has been defined by White (1993) as the saturated interstitial areas beneath the streambed, and into the stream banks, that contain some proportion of channel water, or that have been altered by channel water infiltration. Beyond this point the water contained within the interstices is referred to as groundwater within the phreatic zone. Thus the depth of the hyporheic zone and the points where the hyporheic and phreatic zones merge vary from reach to reach and are unknown in most rivers.

The physico-chemistry of groundwater associated with braided rivers is dictated by a combination of the proximity of the recharge reach of the river from which they are derived and catchment morphology and geology (Rosen 2001, White et al. 2001). With increasing residence time of water within the aquifer hyodrochemistry becomes more like that of true groundwater. White et al. (2001) made measurements in wells positioned at increasing distances from recharge zones of the Waimakariri River and showed an increase in Cl^-, HCO_3^- and nitrate-nitrogen away from the river. Similarly, Scarsbrook and Fenwick (2003) found that dissolved oxygen concentration and temperature were lowest in groundwater further away from the Ngaruroro and Waipawa rivers in Hawkes Bay. Gray et al. (2006) sampled groundwater beneath and adjacent to the lower Waimakariri River and found that temperature and electrical conductivity were highly variable compared to spring sources in the upper river and did not show a correlation with surface water. Temperatures were more similar to those in the main channel, probably reflecting the recent source of groundwater and residence time within the substrate. See (Fig.7) for a summary of this information.

Fenwick et al. (2004) reviewed the general characteristics of groundwater habitats, many of which are probably similar to those of alluvial aquifers of braided rivers. As a consequence of the lack of light, and thus photosynthetic activity, almost all organic matter is imported. Secondly, groundwater habitats are contained within an immoveable matrix of alluvial deposits. The size, chemical reactivity and heterogeneity of the matrix pores dictate many of the physico-chemical characteristics of alluvial groundwater. In New Zealand, the generally inert nature of the substrate and the constricted pore space are associated with slow temporal changes in water chemistry.

Several studies have considered the physico-chemistry of the shallower, hyporheic zones of braided rivers (Burrell 2001; Fowler and Scarsbrook 2002; Olsen and Townsend 2003). Olsen and Townsend (2003) found that up-welling water in Otago streams was consistently colder than down-welling water in both winter and summer. They also noted that interstitial water contained greater dissolved oxygen, ammonium and soluble reactive

phosphorus in winter than in summer. Fowler and Scarsbrook (2002) observed lower temperatures and higher conductivity in up-welling stream water in the lower North Island, but no difference between dissolved oxygen levels. They also noted variation between surface water and hyporheic pH, although the relationship was not consistent between rivers. Strong gradients of physicochemical factors exist within the hyporheic zone and are regulated by patterns of up- and down-welling water at both the reach and pool-riffle scale (Collier and Scarsbrook 2000).

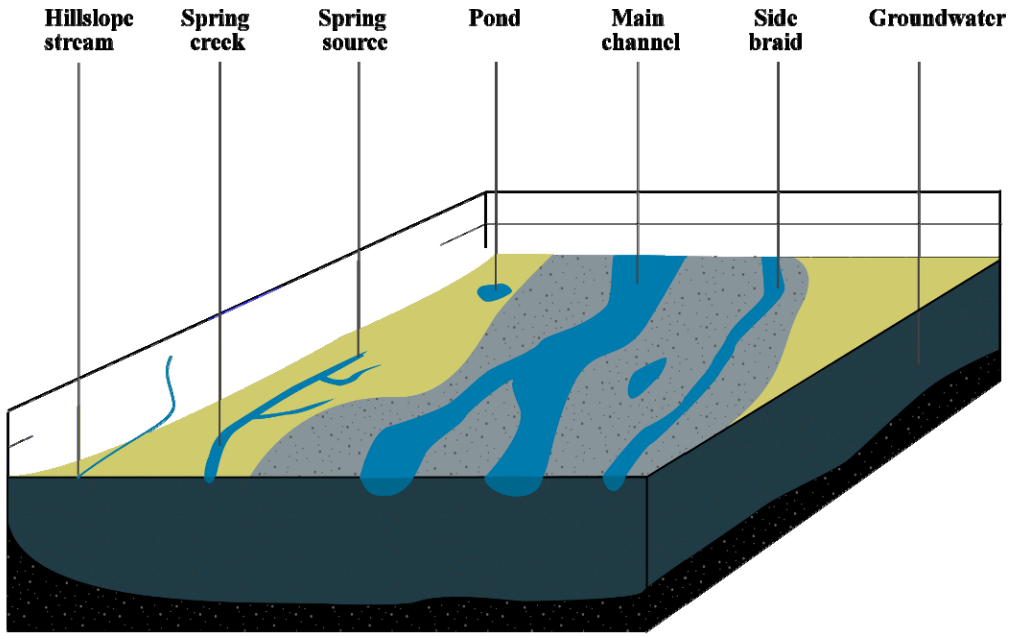
3.4 Floodplain ponds

Lentic habitats on braided river floodplains may form in two ways (Fig. 6). Firstly, an area of floodplain surface that intersects the water table may create a pond. As a result of its dependence on water table height the site may alternate between dry, standing water, and being connected with flowing surface water.

Alternatively, depressions in the floodplain surface may be perched above the water table, but accumulate surface runoff water and form ponds of varying permanence. Very little is known specifically about the habitat conditions in New Zealand floodplain ponds although it is thought that those fed by groundwater are more permanent than those reliant upon rainwater or floods. Mosley (1983b) observed very high temperatures (>26^{o}C) in floodplain ponds of the Ashley River, but did not identify the source of the water.

Figure 6. A groundwater-fed floodplain pond on the Waimakariri River floodplain.

In the Tagliamento River, Italy, floodplain ponds were numerous in the bar-and-island braided reaches of the river, but were absent from constrained and regulated sections. The number of ponds appeared to depend upon sediment grain size, river corridor width, slope of the corridor and degree of river regulation e.g. flood works. Ponds were found to be highly heterogeneous habitats, particularly in terms of thermal and water level fluctuations bought about by groundwater up-welling (Karaus 2004; Karaus et al. 2005). Thus, the physical conditions within each floodplain habitat are broadly predictable and are summarised in Fig. 7.



	Hillslope stream	Spring creek	Spring source	Pond	Main channel	Side braid	Groundwater
Temperature	Seasonally variable	Stable	V. stable	Seasonally	Highly variable	Highly variable	V. stable
Turbidity	Seasonally variable	Low	V. low	-	Highly. variable	Variable	V. low
Physical disturbance	Variable	Low	V. low	V. low	Highly variable	Highly variable	VV. low
Permanence	Variable	High	High	Variable	Variable	V. variable	High

Figure 7. A summary of the physical conditions within the habitat types of a braided river floodplain.

3.5 A holistic view of floodplain habitats

Whilst braided river floodplain habitats may be physically and biologically distinct they are not discrete habitats. The braided river hydrological system consists of a single body of water moving at variable speeds along the valley (Woessner 2000; Poole et al. 2004). Both surface and subterranean habitats are linked, such that the river corridor forms a 3-dimensional mosaic of connected habitats. This dynamic mosaic is characterised by the interrelated themes of ecotones and connectivity between habitats. Ecotones are transition zones between adjacent patches of dissimilar condition (Ward et al. 1999b) and they occur at a range of scales, at the boundaries between: terrestrial and aquatic environments, groundwater and surface water, and zones within a single habitat 'type'. The importance of ecotones to biodiversity has been a recurrent theme in ecology over

recent years (Hansen and di Castri 1992; Lachavanne and Juge 1997). Hydrological connectivity, the transfer of water between patches within the mosaic, has profound implications for a braided river. It regulates the functional and structural attributes of habitat patches and ecotones, giving rise to a high diversity of lentic, lotic and semi-aquatic habitat types (each at various successional stages) that are embedded within the floodplain habitat mosaic. The often extreme heterogeneity in habitat conditions within braided river floodplains is a major contributing factor to the high biodiversity levels found within them. This complex, spatio-temporally dynamic mosaic provides a physical habitat template that exerts variable degrees of influence upon its biotic communities that inhabit it.

4.0 Biotic communities

Despite the physically unstable nature and high turnover of habitats found on braided river floodplains, their biological communities persist, probably because the relative proportions of each habitat remain roughly constant (Arscott et al. 2002; Hauer and Lorang 2004; Latterell et al. 2006). Consequently, mobile taxa in particular persist within a floodplain, and form part of a meta-population within the river system (Begon et al. 1996). Furthermore, the existence of habitats at different successional stages provides a highly diverse mosaic of flooplain habitats, each with its own distinct biological community.

Braided rivers in New Zealand support diverse communities of plants, invertebrates, fish and birds, both introduced and native (NCCB 1983; O' Donnell and Moore 1983; NCCB 1986; Peat and Patrick 2001). A number of indigenous taxa are recognised as braided river specialists and are restricted to, and dependent upon, braided river habitats. Among braided river birdlife, the wrybill (*Anarhynchus frontalis)*, pied and black stilts (*Himantopus* spp.), banded dotterels (*Charadrius bicinctus)*, oystercatchers (*Haematopus* spp.), plovers and some gulls (*Larus* spp.) all use braided rivers during some portion of the year and during some stage of their life cycles (Pierce 1979, 1983; Maloney et al. 1997; Caruso 2006). Introduced salmonids, native bullies (*Gobiomorphus* spp.) and Galaxiidae are relatively common within braided river habitats. Spring-fed streams are

particularly important as spawning sites for trout and salmon, and a number of rare non-migratory galaxiids also appear to be restricted to braided rivers (Townsend and Crowl 1991). In particular the longjaw (*Galaxias prognathus*), bignose (*G. macronasus*) and alpine (*G. paucispondylus)* galaxiids have distributions restricted to braided river habitats within several large south and central Canterbury rivers (Peat and Patrick 2001, McDowall 2000; Bowie 2004).

Whilst plant and terrestrial invertebrate communities have been well documented, and include threatened species such as the native forget-me-not (*Myosotis uniflora*) and the robust grasshopper (*Brachaspis robustus)*, there is less information on the aquatic invertebrate communities of braided rivers. Percival (1932) referred to the main channels of large braided rivers such as the Waimakariri, Rangitata and Waitaki as 'relative (biological) deserts', owing to the extreme substrate disturbance during floods. Similar views have been reported for the main channels of braided rivers, citing low diversity, low abundance and a high degree of domination by well adapted taxa (Hirsch 1958; Winterbourn et al. 1971; Pierce 1979; Sagar 1986). More recent studies however, have identified a wide range of braided river floodplain habitats and demonstrated the potential of some of them as biodiversity hotspots (Digby 1999; Gray et al. 2006).

4.1 Main channel invertebrate communities

Various spatio-temporal patterns and drivers of community composition have been recognised within New Zealand braided rivers. For example, physical disturbance has been shown to structure many stream benthic communities (Percival 1932; Death 1991; Winterbourn 1997). In the South Island, despite rivers experiencing aseasonal and unpredictable patterns of rainfall and flooding, consistent seasonal fluctuations in braided river invertebrate communities have been observed. Investigations of faunal densities in Canterbury braided rivers have reported a consistent pattern of high abundance during winter followed by a spring decline, after which density gradually recovers to winter levels (Sagar 1986; Scrimgeour and Winterbourn 1989; Sagar and Glova 1992). An inverse seasonal pattern however, was reported for the Waipawa River and for Timber Creek in Otago. Abundance and taxonomic richness were lowest in winter and peaked in

summer (Scarsbrook and Townsend 1993; Fowler and Death 2000). These differences may reflect hydrological differences between alpine-sourced rivers and foothill-sourced ones. In spring, orographic rain, often combined with snow melt, produces major floods in the alpine-fed Canterbury rivers, whilst discharge is most stable during winter when precipitation occurs as snow in the upper catchments. In contrast, the Waipawa River and Timber Creek catchments are situated in the rain shadow of their respective main divides and major floods result from southerly weather fronts, which are more common in winter. Concomitantly, invertebrate abundance responds to the warmer summer temperatures and increased algal biomass that occurs during the stable summer flows of these catchments (Scarsbrook and Townsend 1993; Fowler and Death 2000). In Italy, faunal densities in the Tagliamento River peaked in summer (August), but achieved their lowest levels after autumn floods (Arscott et al. 2003), indicating that they are also structured by discharge events.

Several studies report the overriding influence of discharge variability, and particularly discrete floods, on main channel invertebrate communities. In the lower Rakaia River invertebrate abundance was inversely related to antecedent discharge, and was lowest following severe floods (Sagar 1986). Similarly, taxonomic diversity and the biomass of invertebrates were greatest during stable flow periods in winter and lowest following spring floods. In the Rakaia River, floods in excess of 400 m^3/s caused significant bed-load movement resulting in catastrophic invertebrate drift, physical damage to individuals and a reduction in resource supply (Sagar 1986). Following an extreme flood (454 m^3/s) in the Ashley River, benthic communities were reduced when water velocities reached the threshold needed to move small cobbles (at a discharge >30 m^3/s) (Scrimgeour and Winterbourn 1989). However, despite the occurrence of several floods >30 m^3/s, over the following 132 days, benthic invertebrate communities rapidly recovered to pre-flood levels (Scrimgeour et al. 1988).

Invertebrate communities can recover rapidly following flood disturbance in braided rivers, for example, Sagar (1986) recorded a doubling of invertebrate abundance in the Rakaia River during a 2-week period of stable flow in winter. Various recolonisation

mechanisms have been proposed for post-flood stream invertebrates. Drift downstream, migration upstream within the water column, migration from some flood refuge (e.g. peripheral floodplain habitats) and aerial oviposition (Williams and Hynes 1976; DoleOlivier et al. 1997; Gayraud et al. 2000; Holomuzki and Biggs 2000) have all been cited as possible recolonisation mechanisms. The persistence and resilience of benthic invertebrate populations has been examined in numerous stream habitats and the varying roles of each recolonisation method assessed for the habitat and its taxa (Scarsbrook 2002). In a spatially heterogeneous environment, the presence of refugia and source patches of colonisers should reduce the effects of disturbance (Townsend 1989). These patches can occur at a range of scales. Stable substrate patches (Biggs et al 1997; Francoeur et al 1998; Matthaei et al 2000) (at the micro-scale), spring creeks and tributaries (Scrimgeour et al 1998) (at the meso-scale), and the location of a reach (i.e. in a floodplain versus being constrained) (macro-scale) all play a role in the persistence and resilience of stream communities and speed post-flood recovery in braided rivers (Scarsbrook and Townsend 1993).

In the alpine-sourced Rakaia River, Pierce (1979) reported extremely high post-flood abundances of *Deleatidium* spp. in isolated pools and backwaters that could not be explained by recent oviposition and/or egg hatching. Similarly, Scrimgeour et al. (1988) were unable to provide an adequate explanation for the post-flood abundance of *Deleatidium* larvae in the foothill sourced Ashley River. However, immediately after the flood they found high abundances and diversity of taxa in peripheral floodplain habitats, which might have acted as sources of colonisers post-flood. In the foothill sourced Kye Burn in Otago, benthic invertebrates were observed in the inundated floodplain during a flood (Matthaei and Townsend 2000a). Matthaei and Townsend (2000a) indicate that these individuals probably returned to the main channel, presumably by drifting in the receding flood waters. Another possible flood refugium considered by Matthaei et al. (2000) was the matrix of stable substrates within the streambed. Both taxonomic richness and abundance were higher on stable substrates post-flood, suggesting that some invertebrates actively seek stable substrates. Main channel invertebrates may also use the hyporheic zone as a refuge. In an experimental flume, *Deleatidium* nymphs were shown

to enter deeper sediments with incremental increases in discharge (Holomuzki and Biggs 2000), and in the Kye Burn *Deleatidium* spp. was found to be more abundant in depositional than scour patches (Matthaei and Townsend 2000b), suggesting the use of the shallow hyporheic as a flood refuge. However, several conflicting studies about the use of the hyporheic zone by invertebrates as a flood refugium can be found in the literature and any possible role the hyporheic plays as a flood refuge is still unclear.

The wider floodplain also includes other possible flood refugia such as less disturbed side braids, upstream reaches, springs, hillslope streams and ponds. These habitats may act as sources of new colonisers rather than as potential refugia for inhabitants of main channel braids during floods (Ward et al. 1999a)

A compilation of 18 papers (Appendix 1) recording taxonomic richness and abundance of aquatic macroinvertebrates in the main channels of braided rivers in New Zealand shows a mean taxonomic richness of 25 (SE ± 4) and a mean density of 2, 598 individuals/m^2 (SE ± 703). Aquatic invertebrate communities were dominated by the leptophlebiid mayfly *Deleatidium* spp., chironomids and elmid beetles. The sandfly *Austrosimulium*, the stonefly *Zelandobius*, Eriopterini (Diptera) and predatory hydrobiosid caddis were all relatively common. Although the highest richness (56 taxa) was recorded in the Waipawa River on the East Coast, North Island, many of the taxa found constituted <1% of any sample (Fowler and Death 2000). This is probably not surprising as many taxa might be represented by a few individuals that drift into the mainstem from more stable tributaries and the hyporheic zone (Winterbourn 1997; Kilroy et al. 2004). Collation of the results from six surveys of the main channels of the Tagliamento, Roseg, Brenno and Lesgiuna rivers showed mean richness of 43 taxa (SE ± 9) and mean density of 59, 179 (SE ± 36, 159) individuals/m^2, both values being higher than those found in New Zealand (Ward et al. 1999, Brunke 2002, Burgherr et al. 2002, Arscott et al. 2003, 2005). Several issues may affect these comparisons. For example, many workers use variable levels of taxonomic resolution for some of New Zealand's most speciose groups e.g. leptophlebiids, hydrobiosids and chironomids, while a number of New Zealand studies may have also been undertaken prior to more recent advances in taxonomy. In addition

the extremely high macroinvertebrate density in some European braided rivers partly reflects the use of a smaller sampler mesh size (100 μm), compared to that used in New Zealand (minimum 200 μm, average 350 μm). Small chironomids dominated the European results and meiofauna were included. Furthermore, the high variation in abundance in the European data is exacerbated by the particularly low densities reported for the glacier-fed Roseg River in Switzerland, were faunal densities more similar to those of New Zealand's braided rivers (Burgherr et al. 2002).

The mean taxanomic richness found in New Zealand braided rivers, both alpine and foothill-sourced, was 25 ± 4 (Appendix 1), which is considerably lower than the 61 taxa recorded in forest streams by Rounick and Winterbourn (1982), and the 79 taxa found in springs and 53 taxa found in hillslope tributary streams by Gray et al. (2006). The density of individuals in braided river main channels (2, 598 ± 703 individuals/m^2) was also considerably lower than that recorded for spring sources (22, 982 ± 3 413 individuals/m^2), mossy forested streams (218, 400 ± 15 100 individuals/m^2) and urban streams (25, 000 ± 8 500 individuals/m^2) (Suren 1991; Blakely and Harding 2005).

European studies of longitudinal patterns in the invertebrate communities of the main channels of braided rivers have revealed some striking patterns (Arscott et al. 2003, 2005). The composition of headwater benthic communities was more stable over time compared to downstream communities. Faunal diversity, however, was highest at each end of the river continuum. More specifically, Chironomidae and *Baetis* mayflies showed little change in abundance along the river, but stoneflies were mostly restricted to the upper reaches and Crustacea, nematodes and oligochaetes became more common in the lower reaches. The lowest density recorded in the Tagliamento River was 433 ± 158 individuals/m^2, for an island-braided floodplain reach morphologically similar to those in many New Zealand braided rivers.

In a comparison of the benthic fauna in the mid-reaches of the Rakaia River with the upper reaches of the Waitaki River, Pierce (1979) recorded that both communities were dominated by *Deleatidium* spp. and predatory and cased caddis larvae. Despite low

densities in both rivers the mean density of *Deleatidium* was higher in the upper Waitaki River (176 individuals/m^2) than in the middle Rakaia (85 individuals/m^2) and the free-living predatory caddis common in the Rakaia were replaced by case-dwelling Leptoceridae and Conoesucidae in the Waitaki River. Waitaki River invertebrate communities were less temporally variable in composition and abundance than those in the Rakaia. Sagar (1986) investigated invertebrate communities in three longitudinally arranged reaches of the lower Rakaia River and found taxonomic diversity and abundance were greatest in the lower reaches during winter but, showed no significant longitudinal change during summer. The greater lower reach diversity was attributed to longitudinal changes in river morphology leading to greater habitat heterogeneity and reduced substrate movement.

Benthic communities of braided rivers are often dominated by generalist taxa which may exhibit multivoltinism (multiple broods annually), asynchronous lifestyles, refuge-seeking behaviour and the ability to recolonise a denuded substrate. Regular flooding reduces the quantity and quality of epilithic food resources (Scrimgeour and Winterbourn 1989) and the shifting wetted bed of a braided river requires invertebrates to be able to exploit the resulting very thin organic layers on stone surfaces for food (Sagar 1983; Fowler 2004). High fecundity, good dispersal ability and multivoltinism may allow surviving and recolonising invertebrates to rapidly repopulate stream substrates. Coupled with an asynchronous lifestyle, these adaptations ensure that at any time of year there are individuals at various stages of the life cycle, making survival of a disturbance event by some individuals very likely (Winterbourn 1974; Scrimgeour et al. 1988; Scrimgeour and Winterbourn 1989). Specific taxa exhibit different behavioural strategies in response to increases in discharge (Holomuzki and Biggs 2000). Dorso-ventrally flattened, clinging but mobile taxa such as *Deleatidium* spp. are rarely dislodged from a stable substrate compared to cased caddis and the hydrobiid snail *Potamopyrgus antipodarum* (Holomuzki and Biggs 2000). However, when substrate particles move, *Deleatidium* spp. may enter the drift voluntarily (Matthaei and Townsend 2000a). In contrast, cased caddis and *P. antipodarum* rely upon downward movement within the substrate and the protection offered by their respective case or shell. In a highly disturbed riverbed with

highly mobile substrate, drifting downstream into areas of lower current velocity is likely to be a more effective strategy than local-scale movements or reliance on a hardened covering. Hence, Potamopyrgus and cased caddis are not often found in rivers with frequently disturbed beds. Taxa of braided river main channels such as *Deleatidium* spp., *Zelandoperla* spp., Chironomidae, Oligochaeta, Eriopterini and Elmidae all share the trait of effective flood avoidance by drift, which also permits rapid recolonisation of denuded substrates.

A fall in river stage height, or lateral movement of braided river channels, may result in the temporary drying of a section of streambed. The processes by which existing channels get cut off and dry are described in detail by Digby (1999) and Rundle (1985). The response of invertebrates to the re-wetting of these channels has been described in several studies, which found that they can quickly colonise the newly wetted areas (Sagar 1983; Malmquist 1991; Fowler 2004). However, the rate and mechanism of recolonisation may depend on whether the dry period coincides with the emergence and oviposition of adults, since species whose hatching period overlaps the dewatered period may be slow to recover to post-dewatering levels. Some insect species can also enter diapause to allow eggs to survive dewatering (Storey and Quinn 2007). Recolonisation after dewatering is probably predominantly through drift, though vertical migration and aerial oviposition may all occur (Williams and Hynes 1976). In the Rakaia River, recolonisation of re-watered substrate took 33 days in winter but, only 15 days in summer, and was principally driven by discharge fluctuations and the resulting drift (Sagar 1983; Sagar and Glova 1992). In an analogous study on the East Coast of the North Island, species diversity recovered after only 7 days (Fowler 2004). Abundances of taxa were slower to recover, especially at sites that had been dry for moderately long periods of time (>6 weeks). The fastest colonisers were chironomids and elmid beetles, and they were also initially dominant at sites that had been dewatered for a longer period of time (Fowler 2004).

Another important driver of benthic invertebrate community structure is in-stream biofilm. Biofilm consists primarily of algae (or periphyton), but also fungi and bacteria,

as well as organic and inorganic particles (Rounick and Winterbourn 1983; Biggs and Kilroy 2004a). Biofilm is frequently the basal food resource for invertebrates and, therefore plays a very important role in structuring communities. The periphyic component of biofilm is influenced primarily by physical and biological factors that operate at a local scale; light, flow regime, wave action, nutrients, temperature and invertebrate grazers (Biggs and Kilroy 2004). Both high and low flows can affect biofilm by physical abrasion and desiccation, respectively. Biggs and Close (1989) and Biggs (2000) found that flooding regimes and nutrient levels explained 63% and 62% of the variance in periphyton communities in two separate studies of braided rivers. The loss of biomass during a flood event depends upon flow velocity, the stability of bed sediments and the ability of algal species to resist "sloughing" from the substrate. Consequently, in braided river main channels periphyton and biofilm can be very sparse, although areas with lower velocities and stable substrates may have relatively high periphyton biomass (Biggs and Close 1989). In the Ashley River the organic layer (epilithon) recoved rapidly to post flood levels despite the occurrence of subsequent minor floods, a pattern which was mirrored by the invertebrate community (Scrimgeour et al. 1988). However, despite the reliance of many invertebrates on highly variable epilithic food resources, many taxa (particularly *Deleatidium*) are able to survive on very low levels of algal biomass and are unlikely to be food limited in streams (Scrimgeour and Winterbourn 1989). De-watering can also have an effect upon biofilm depending partly on what species are present as they show variable abilities to withstand desiccation (Mosisch 2001). In the Waipawa and Tukituki rivers in Hawkes Bay, the recovery of algal biomass was slower in channels that had been subject to longer periods of de-watering as there was no persistent algal standing crop from which to re-establish algal communities (Fowler 2004).

4.2 Spring invertebrate communities

The earliest recorded survey of a spring in a New Zealand braided river system was of the Glennariffe Stream, a spring-fed tributary of the Rakaia River. Average density of benthic fauna was 2618 individuals/m^2, 50% of the community were mayflies and 40% were conoesucid caddis (Boud et al. 1959). Early reports also indicated the presence in

springs of some unusual taxa, such as the phreatic flatworm *Prorhynchus putealis* (Percival 1945). However, until recently alluvial springs on braided river floodplains have been largely ignored ecologically. This dearth of studies has been rectified to an extent by a number of studies, especially in the South Island (Death 1991; Death and Winterbourn 1994 and 1995; Digby 1999; Gray 2005; Gray et al. 2006), but also in the North Island (Barquin 2004).

The paucity of studies on the diversity of alluvial springs makes nationwide and international comparisons difficult (Appendix 2). However, of 5 New Zealand studies, undertaken in the Waimakariri River catchment, higher invertebrate taxon diversity was found (mean 66 ± 8) than in the overseas studies (mean 33 ± 12). In New Zealand, taxonomic diversity and abundance seem to be higher on average in braided river springs than in adjacent main channels and hillslope streams (Rounick and Winterbourn 1982; Death 1991; Gray et al. 2006) and taxonomic richness and the community composition of springs appears to be more stable over time than in more disturbed habitats (Death 1991). Furthermore, Digby (1999) found that secondary production in a perennial seepage stream was an order of magnitude higher than in the main channel of the Rakaia River.

Death (1991) suggested that both density and diversity of invertebrate communities decline downstream from a spring source. However, while Barquin (2004) found an increase in taxonomic richness with distance downstream, Gray (2005) observed a decrease, although the pattern was weak in both studies. Neither study found any longitudinal change in invertebrate abundance, but both reported an increase in filter-feeding taxa away from the source. Both studies concluded that the effect of temperature stability at the source and increased temperature variability downstream were not critical controllers of invertebrate community composition as had been suggested by Northern Hemisphere studies (Minshall 1968; Ward and Dufford 1979; Glazier 1991), but instead, they suggested that a longitudinal decline in substrate stability, site-specific substrate differences and biological interactions were likely play more important roles (Barquin 2004; Gray 2005).

Gray (2005) identified two additional factors that affect invertebrates in springs and spring creeks. At spring sources, dense macrophytes supported communities dominated by chironomids and the hydrobiid snail *Potamopyrgus antipodarum.* But, after removal of macrophytes, communities shifted towards dominance by *Deleatidium* and conoesucid caddis. Successional stage, or time since the last catastrophic disturbance, also influenced spring fauna composition. The inter-montane basin reaches of the Waimakariri River are thought to re-work their entire floodplains approximately every 250 years (Reinfelds and Nanson 1993), implying that their springs may be at different stages along a 250 year successional gradient. In the Waimakariri, Gray (2005) found older springs had a higher proportion of non-insect taxa than younger springs, although there was considerable variation within age categories.

Many of the taxa found in New Zealand springs are widely distributed and not restricted to spring habitats. This differs from findings in the Northern Hemisphere, where obligate spring taxa seem to dominate spring habitats (Death et al. 2004). However, recent surveys across New Zealand have revealed a high diversity of previously undescribed hydrobiid snails in springs and seepages which may yet prove to be crenobionts (spring specialists) (Scarsbrook and Fenwick 2003). Springs are not the only known surface habitats where several groundwater taxa have been collected. The amphipods *Paraleptamphopus* spp. are also common in West Coast, forested streams, however it is likely that with an increase in the taxonomic resolution of this group that spring specialist species will be found. However, the amphipod *Phreatogammarus fragilis* and the flatworm *Prorhynchus putealis* have very limited surface habitats outside of springs and spring creeks. More importantly, the presence of springs within the braided river corridor supports a higher number of taxa than exist in the unstable main channels (Gray 2005).

4.3 Groundwater and hyporheic invertebrate communities

Studies of groundwater habitats in New Zealand fall into two separate groups, both of which are relevant to braided rivers; those of the shallow hyporheic zone and those of the deeper phreatic zone. Studies of the hyporheic zone of braided rivers are most common and include those by Scarsbrook (1995), Fowler (2000), Burrell (2001), Fowler and

Scarsbrook (2002), and Olsen and Townsend (2003) but, there have been very few investigations that included the deeper aquifer (see Scarsbrook and Fenwick 1993). These deeper groundwater systems may represent the greatest aquatic volume of the river and therefore represent a large, understudied component of the ecosystem (Stanford and Ward 1988, 1993).

The benthic fauna can be classified according to its degree of affinity with groundwater or hyporheic habitats (Gibert et al. 1994; Collier and Scarsbrook 2000; Scarsbrook et al. 2003). A number of terms have been developed to describe taxa that occur in these subterranean zones, in particular 'stygophiles' are organisms which have an affinity for subsurface zones, and are subdivided into 'occasional', 'amphibitic' and 'permanent' subgroups. 'Occasional' taxa include the caddis *Olinga feredayi*, which has been found at depths of at least 30 cm in several streams and may use the hyporheic zone as a refuge from flood disturbance (Adkins and Winterbourn 1999; Burrell 2001). 'Amphibites'or amphibionts are species that spend their entire larval life within the hyporheos but return to the surface to complete their life cycles (Stanford and Ward 1993). Presently no amphibionts have been confirmed to occur in New Zealand, although *Spaniocercoides cowleyi* may be one (Cowie 1980; McLellan 1984; Winterbourn et al. 2006). 'Permanent' hyporheos dwellers in New Zealand include some nematodes, oligochaetes, mites, copepods, ostracods and cladocerans (Scarsbrook et al. 2003). Other hyporheic specialists may exist, for example the unpigmented, eyeless *Namanereis tiriteae*, a freshwater polychaete, which has been found in in the North Island (Winterbourn 1969; Fowler 2000). The final group, the 'stygobites' are true groundwater species that are blind, unpigmented and physiologically and morphologically adapted for groundwater life (Gibert et al. 1994). They are ubiquitous in alluvial and karst aquifers and include 'phreatobites' which are restricted to deep alluvial aquifers such as those beneath the Canterbury Plains. Phreatobite communities consist primarily of amphipods, isopods, beetles, snails and mites and although apparently diverse, little research has been carried out on them in New Zealand, and more taxonomic and ecological studies are needed (Sinton 1984; Fenwick 1987; Scarsbrook et al. 2003; Fenwick et al. 2004). The abundance of fauna within alluvial aquifers is difficult to measure owing to sampling

difficulties, but abundance may increase where nutrients reach the aquifers (Sinton 1984; Fenwick 1987; Fenwick et al. 2004).

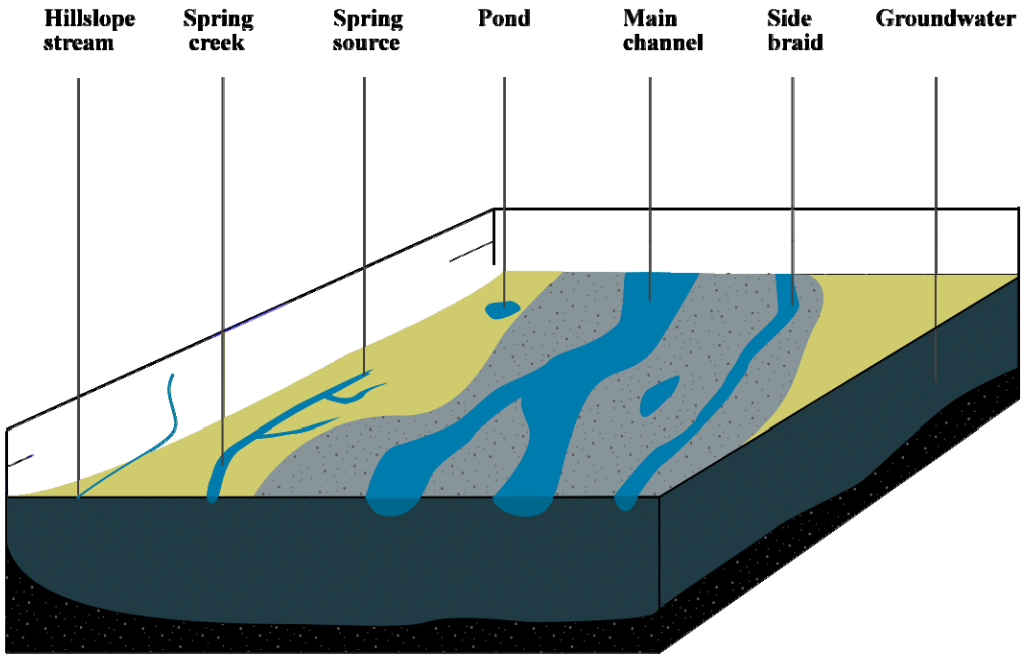
New Zealand's shallow hyporheic zones constitute an interface between surface water and groundwater systems, mediating the movement of energy, matter and individuals between the two zones, and providing habitat for a diverse range of aquatic taxa (Collier and Scarsbrook 2000). The presence of large numbers of aquatic invertebrates in the hyporheic zone has implications for the study of ecosystems, especially large braided rivers with an extensive hyporheic zone. Sampling of the surface benthos underestimates the true number of invertebrates in a river (Adkins and Winterbourn 1999; Huryn 1996) and ignores important vertical colonisation pathways (Williams and Hynes 1976). Internationally, most hyporheic research has been carried out in small streams, although significant, large scale studies have been done in large braided rivers systems such as the Flathead River in Montana (Stanford and Ward 1988). In New Zealand, braided rivers have been targeted in several studies. Burrell (2001) conducted hyporheic surveys and experiments in the braided Ashley and Waipara Rivers in Canterbury, whilst Olsen et al. (2001) and Olsen and Townsend (2003) worked in the Kye Burn in Otago and Fowler (2000) on the Makaretu, Tukituki and Waipawa Rivers in the North Island.

The effect of vertical hydrological exchange (VHE), i.e. up-welling versus down-welling of water, on invertebrate community composition has been assessed in the Kye Burn, Waipawa, Tukituki and Makaretu Rivers. In the Kye Burn, taxonomic richness did not differ between up- and down-welling areas (Olsen and Townsend 2003), although eveness was greater at up-welling's. In the North Island richness was greatest at down-welling sites owing to high numbers of epigean taxa, and possibly the lower taxonomic resolution of hypogean taxa (Fowler and Scarsbrook 2002). In the Kye Burn, invertebrate density was greatest in the near-surface hyporheic sediment, and sediment composition and VHE was the most influential driver of invertebrate communities, which were dominated by early instar leptophlebiids and asellotan isopods (Olsen et al. 2001; Olsen and Townsend 2003). Hyporheic samples taken from the Ashley and Waipara Rivers in Canterbury by Burrell (2001) were also dominated by epigean taxa, especially

harpacticoid copepods, and insect taxa such as Chironomidae and Polycentropidae. Hyporheic communities increased in abundance where organic matter was more abundant although the effect declined with increasing depth (Burrell 2001).

4.4 Floodplain pond communities

The invertebrate communities of floodplain ponds have received little attention. The presence of a dytiscid beetle *Huxelhydrus syntheticus* and a species of stratiomyid in temporary riverbed ponds in the Waimakariri River catchment has been noted by Winterbourn et al. (2006), while Scrimgeour et al. (1988) observed the larvae of *Aoteapsyche*, *Hydrobiosis* and *Psilochorema* in a stagnant pool 150 m from the main channel of the Ashley River. These taxa had been absent from the main channel following a large flood, but after a subsequent flood, which re-connected the pool with a side braid, the taxa were once again present in the braid below the pool. These casual observations suggest that pools created during high flows may act as sources of colonists when they are reconnected to the main channel. In the Tagliamento floodplain, Italy, a larger percentage of aquatic taxa was restricted to parafluvial ponds, than the main river channel, but the similarity between pond communities was quite low, reflecting high between pond heterogeneity (Karaus 2004, Karaus et al. 2005). The information in section 4 is summarised in (Fig. 8)



	Hillslope stream	Spring creek	Spring source	Pond	Main channel	Side braid	Groundwater
Taxa richness	Medium	V. high	High	Variable	Low	Low-medium	Low (poor resolution)
Abundance	Medium	High	High	Variable	Low	Low -medium	Unknown
Species evenness	High	High	Medium-high	High	Low	Med-low	Unknown
Characteristic taxa	*Nesameletus* *Austroclima* *Oniscigaster* *Edpercivalia*	*Pycnocentrodes* *Deleatidium* *Zelolessica* *Potamopyrgus*	*Prorhynchus* *Phreatogammarus* *Paraleptamphopus* Isopoda	*Anisops* *Xanthocnemis* *Huxelhydrus* *Rhantus*	*Deleatidium* Elmidae Eriopterini Free-living Caddis	*Deleatidium* Elmidae Chironomidae Eriopterini	Amphipoda Isopoda Ostracoda Acarina

Figure 8. The biological characteristics of braided river floodplain habitat types in New Zealand.

5.0 A holistic perspective of braided rivers

Braided river floodplains have been identified as hotspots of aquatic biodiversity in the Northern Hemisphere (Ward et al. 1999b), and although relatively few studies have been conducted in New Zealand, this seem likely to be the case here too (Gray et al. 2006). The high biodiversity on braided river floodplains may be attributable in part to high habitat heterogeneity and the large size of many of these river systems. Despite the reputation of braided rivers as harsh physical environments, communities in a confined single-channel river might suffer greater 'disturbance' than those in a braided river when

exposed to a flood of equivalent magnitude (Mosley 1982a). Braided river floodplains moderate the physical and biological effects of floods by dispersing the flood water's energy over a greater area, and the presence of an extensive mosaic of habitats provides refugia and sources of recolonists. In contrast a confined river channel provides fewer refugia for invertebrates or internal sources of colonisers, and the full scouring force of a flood is concentrated within the single channel. Thus, despite the position of a braided river's main channel at the extreme of a disturbance gradient (Scarsbrook and Townsend 1993), braided river floodplain invertebrate communities in total may be more persistent than those within a constrained channel (Fowler and Death 2000). Winterbourn's (1997) suggestion that South Island mountain streams are "both stable and disturbed" can probably be extended to the braided rivers of the North and South Islands. Whilst, disturbance events may spatially re-arrange and temporally reset individual floodplain habitats, the shifting mosaic ensures that representatives of each habitat persist at all times.

6.0 Threats and pressures

Braided rivers and their associated floodplains provide services and resources to people in a variety of ways beyond their role as conduits of water and gravel to the sea. As New Zealand's population increases the magnitude of pressures and demands for use of our braided rivers will continue to grow. In this section we briefly review the major pressures on braided rivers in New Zealand.

6.1 Impoundment

Both the surface water and groundwater associated with braided floodplains are variably competed for by hydroelectricity generators, irrigators and municipal water suppliers (Young et al. 2004). In New Zealand a number of major rivers have been impounded for the generation of hydroelectricity, the Clutha, Waitaki, Waikato, Rangitaiki and Waiau rivers all feature at least one dam, and numerous other rivers are subject to flood harvesting or diversion (Henriques 1987). Further flow diversion takes place to supply irrigation demands particularly in the water-short eastern regions. There is a wealth of international and New Zealand literature summarising the general downstream effects of

flow regulation by impoundment (e.g. Henriques 1987, Rosenberg et al. 2000, Young et al. 2004, Graf 2006, Poff et al. 2007). Dams and river diversions have major impacts on downstream aquatic habitat, contribute to the loss of fisheries, modify species distributions and reduce ecosystem services (Pringle et al. 2000; Rosenberg et al. 2000). In particular, the negative impact of flow regulation upon the morphological and successional diversity of flood plain habitats has been highlighted by several workers (Ward and Stanford 1995; Gilvear 2004; Hohensinner et al. 2004; Choi et al. 2005; Hauer and Lorang 2004). Impoundments typically reduce channel-forming flows and longitudinal sediment transport, which in turn reduces the rate of channel migration, and habitat turnover. The effect of flow regulation is similar to that of channelisation, in that it truncates the fluvial system and disconnects the river from its flood plain (Hohensinner et al. 2004). Impounding a river can have marked effects on water chemistry, invertebrates and fish, and on the upstream and downstream transport of organic matter and migratory animals (Pringle et al 2000; Young et al 2004). Benthic invertebrate communities are often drastically altered so that former distributions of riverine taxa become discontinuous (Harding 1992a, 1992b). The distribution and abundance of many fish communities are also significantly impacted by impoundments, which create lentic environments unsuited to most river dwelling fish, and also form barriers to migration of species that spend some of their lives at sea (Young et al 2004).

6.2 Water extraction

Irrigation of farmland, particularly for the dairy industry requires large volumes of water. The effect of water abstraction, particularly on groundwater invertebrate communities, is poorly understood and no studies have looked at depletion effects on stygofauna (Fenwick et al. 2004). Similarly, the effects of groundwater abstraction on surface habitats and biota that receive aquifer recharge are poorly understood (though see Datry et al. 2007). Surface habitats are supplied by water from the upper levels of aquifers and may be quick to dry out at an early stage of water table lowering. Consequently, springs and wetlands may dry out and seawater intrusion may occur in coastal aquifers (Fenwick et al. 2004). The spring-fed sources of the Avon River in Christchurch have moved several kilometers downstream due to water table lowering associated with urbanisation

(Marshall 1973). A compounding effect of irrigation is the leaching of agricultural waste back into the aquifer. The limited biological research done in New Zealand suggests that aquifer ecosystems are likely to be highly sensitive to organic pollution, especially the abundant Crustacea, many of which are sensitive to a range of pollutants (Thomas 1993; Fenwick et al. 2004).

6.3 Low flows

Low flow conditions are a consequence of natural climatic cycles, and are particularly common in rivers in the east of New Zealand. However, impoundments, diversions and water abstraction have markedly increased the frequency, magnitude and duration of low flow events. Low flows are exacerbated or prolonged by man's activities and can have serious negative impacts on the in-stream values of braided rivers. Natural fluctuations in flows may result in shifts in depth, velocity, habitat availability, temperature, dissolved oxygen, nutrient concentration and algal communities, while prolonged reductions in flow may have severe effects on them (Suren and Jowett 2006; Dewson et al. 2007). As flow decreases the amount of habitat available for invertebrates often decreases (Suren and Jowett 2006; Dewson et al. 2007) and in the short term may result in localised increases in invertebrate density as animals are crowded into less habitat (Malard et al. 2006). However, if low flows persist invertebrate densities may decline due to mortality (Cowx et al. 1984). Faunal composition also changes as low flows persist, so that midges, snails and Oligochaetes may become dominant where previously mayflies and caddis dominated (Iversen et al. 1978; Extence 1981; Cowx et al. 1984). As discharge declines some invertebrates may shift their location by drift (Gore 1977). Whereas others may avoid unsuitable conditions by emerging (Greenwood and McIntosh 2004; Harper and Peckarsky 2006). However, if stressful conditions continue many invertebrates will die (Quinn and Hickey 1990). The trophic effects of increased low flows are also highly likely to be detrimental to fish and bird communities that rely on invertebrates for food. Interestingly however, invertebrate communities in the Waipara River responded less strongly to drought than to floods (Suren and Jowett 2006) and the authors concluded that large scale changes to invertebrate communities were unlikely to occur as a result of low flow events in New Zealand streams. Nevertheless, over longer time scales, individual

river communities may show shifts in species composition as low flows become more extreme and prolonged. The Waipara may be atypical as it has been subject to extreme low flows for many years and its present fauna may be low flow adapted.

6.4 Gravel extraction

There do not appear to be any published records on the effects of gravel extraction on the ecology of New Zealand's braided rivers, although inferences can be made from overseas studies. In a review of the physical effects of gravel extraction in several European rivers, river incision was noted both up-stream and down-stream of extraction points along with lateral channel instability and riverbed armouring (Renaldo et al. 2005). Other effects were; alteration of the floodplain inundation regime, a lowering of the valley water table, and the loss or impoverishment of aquatic and riparian habitat. In-stream gravel mining destroyed the heterogeneity of riffles and pools, and may affect the spawning activities of fish (Condole 1994; Cote et al. 1999). Furthermore, the destruction of features such as islands and bars, and the removal of large woody debris reduces in-stream morphological and hydraulic diversity therefore leading to the loss of aquatic habitats (Arsine and Green 2000). We might also expect that the cessation of floodplain inundation and lowering of the water-table would cause a loss or de-watering of peripheral habitats such as floodplain ponds and springs.

6.5 Flood control

The effects of large flood control projects have received considerable attention in New Zealand and overseas (Brunched 2002; Hancock 2002; Hauer and Lorang 2004; Young et al. 2004; Caruso 2006; Scarsbrook et al. in Press). Many large New Zealand rivers have been channelised to create farmland and prevent river migration (Young et al. 2004). Constriction of the active river channel can cause changes in local aggradation and degradation, and can affect the channel's interactions with the aquifer and water supply to springs. A 0.5-m drop in the bed of the lower Motueka River was predicted to reduce summer aquifer recharge by 24% (Young et al. 2004). Furthermore, disconnection of the river from its flood plain tends to reduce habitat heterogeneity at the landscape scale and alter successional dynamics within existing flood-plain habitats (e.g. springs and

floodplain ponds). Following the construction of flood control barriers, extant habitats beyond the barriers are likely to have a reduced probability of disturbance, and tend towards later successional stages, with subsequent implications for biodiversity across the riverscape. Concomitantly, within the flood banks, river constriction means that habitats are likely to experience more regular disturbance and will tend towards earlier succesional stages.

Flood retention works may not have universally negative effects on habitat and biotic diversity. In the lower Selwyn River, Canterbury lateral movements of the river during floods are constrained by flood banks and the planting of riparian willows; and this channel constriction promotes localised riverbed incision, so that the water table is intersected. The resultant ponds and springs may form refugia for fish and invertebrates during summer low flows, although the hypothesis has yet to be tested (Scarsbrook et al. in Press). Gray (2005) noted spring up-welling complexes formed in the lee of flood retention works in the upper Waimakariri River and Kilroy et al. (2004) collected 42 algal taxa in one of these springs, the highest diversity found in any of the 24 springs sampled.

Our review highlights a lack of robust studies on the long-term effects of activities such as gravel extraction and flood bank construction on the morphology, habitat heterogeneity and biodiversity of braided river floodplains.

6.6 Commercial and recreational fisheries

Rivers and their floodplains support significant commercial and recreational fisheries in New Zealand. Maori traditionally exploited a number of freshwater fish, including lamprey, eel, grayling, and whitebait (juvenile migratory galaxiids). The grayling (*Prototroctes oxyrhynchus)* although once abundant is now extinct, and Lampreys (*Geotria australis)* are only harvested intermittently, and not commercially. Whitebait and eels are subject to on-going commercial and recreational harvest by both Maori and European (McDowall 1990c). White baiting is a seasonal recreational activity on most rivers (McDowall 1984). In contrast, angling for introduced salmonids is widespread on

braided rivers throughout much of the country. New Zealand's braided rivers are highly regarded Brown and Rainbow trout fisheries, although the braided rivers of the East Coast of the South Island are better known for their salmon fishery. Salmon run from the sea November to March when angler's queue at the river mouths for a chance to catch them. The salmon spawn in spring creeks and tributaries of rivers such as the Rakaia and Waimakariri (McDowall 1990b). Major threats to fisheries within braided rivers include instream habitat destruction, loss of spawning areas, lethal and sub-lethal effects of low flow and over-harvesting by recreational and commercial fishers (McDowall 1990a; Geist and Dauble 1998; Hancock 2002)

6.7 Pollution

Organic and industrial pollution have been issues affecting braided rivers in the past (Hirsch 1958; Winterbourn et al 1971), but have generally been over-shadowed by impoundment, flood defences and low flows. Rather than the large braided rivers it is the smaller, foothill sourced, rivers, less capable of assimilating/diluting pollutants that are of greater concern. Smaller rivers flowing through areas of intensive agriculture such as the Canterbury or Southland plains face increasing organic pollution from livestock and agricultural activities (Davies-Colley and Wilcock 2004)

7.0 Recreation and landscape values

Braided rivers are also highly valued because of their recreational, landscape and scenic values (Loomis and Walsh 1986). To many people they are part of their cultural identity, central to their recreational activities and integral to their cultural landscape. Many large braided rivers are used regularly for kayaking, jet boating, rafting, four-wheel driving and swimming. They also provide the access points to many mountainous areas and are thus integral to the wilderness experience of people spending time in the mountains. Large river engineering projects, such as hydroelectric schemes and flood defences, are perceived by many recreational users to have a negative effect on the landscape and thus to diminish the value of their experience.

8.0 Management implications and future research

The pressures and threats facing braided rivers have generated a number of management issues (outlined above) and exposed gaps in our understanding of how these ecosystems function. The values, functions and uses of braided rivers are variably dependent upon the integrity of their component parts: the catchment, reach and individual pool or riffle. Future management regimes need to address these issues in order to achieve any efficacy in the conservation of braided river invertebrate fauna.

At the larger catchment scale it is important to maintain the natural flow regime of the river and natural sediment input. Activities such as deforestation, impoundment and extraction of water and gravel can radically alter these factors. At the reach scale flood prevention works, gravel extraction, floodplain vegetation clearance and low flows can have marked effects on floodplain morphology and dynamics further influencing the ecology of floodplain habitats. In particular, further research is needed into the effects of gravel extraction, vegetation presence/absence and the role of large woody debris in braided rivers. Impacts operating at the catchment and reach scale combine to regulate the condition, and diversity of instream habitats. Anthropogenic activities have severe impacts upon the balance of dynamic riverine systems. Consideration of the biodiversity, economic and recreational values of a river system must take into account habitat diversity and functional integrity of the whole system. The 3-dimensional aspect of flood plains, longitudinal linkages and connectivity between adjacent elements in the landscape mosaic should be central features in our biodiversity management of braided rivers (Pringle 1997; Ward et al. 1999; Pringle 2001; Malard et al. 2002; Wiens 2002). Furthermore, recent research has highlighted the importance of floodplain springs as biodiversity hotspots in braided rivers. This finding provides compelling reasons for more active management and protection of braided river springs and spring creeks.

There are a number of areas where further research is needed to improve our understanding of braided rivers.

- Currently there is no coordinated effort to assess spatial biodiversity patterns within braided rivers nationally. Braided rivers occur in 11 of New Zealand's 14

regions (Wilson 2001), but no robust comparisons have been conducted on invertebrate communities within braided rivers across regions. Within and between regions many braided rivers have very different physical conditions, i.e. different sources of flow, geology, catchment vegetation, hydrological regime. Furthermore, a long standing tenet of freshwater ecology has been the existence of a predictable longitudinal arrangement of physical habitats and invertebrate communities (Vannote et al. 1980; Winterbourn et al. 1981). Does this occur in our braided rivers? If so, do taxa and communities vary among braided rivers across differing River Environment Classification (Snelder et al. 2004) classes and eco-regions (Harding and Winterbourn 1997). Answering these questions should enable us to determine the comparative uniqueness of our braided rivers and place their biodiversity values in a nationwide context.

- Many rivers in New Zealand are subject to either invasion of exotic vegetation or its deliberate planting (Hicks et al. 2004). The role of indigenous terrestrial vegetation in influencing floodplain stability has been studied intensively overseas (Gran and Paola 2001, Mosley 2004, Whited et al. 2007), but in New Zealand, we have relatively little understanding of the comparative value of indigenous versus exotic floodplain vegetation to the morphology of braided river floodplains (but see Miller 2006).
- The role of large woody debris in the formation of in-stream habitats is well known in small single-channel streams, but in New Zealand there has been very little work on the physical and ecological roles of large woody debris in braided rivers. Presumably the presence of logs and whole trees increases habitat heterogeneity, carbon resources and potentially biodiversity within a river reach. Research on the role of woody debris should provide new insights into the importance of native vegetation clearance and subsequent invasion by exotic species on the morphology of our riverscapes.
- Although the hydrological links between braided rivers and groundwater have received increasing attention in New Zealand (White et al. 2001), our understanding of the ecology of hyporheic and groundwater systems is less

advanced. Given the pressures and values which are placed upon groundwater resources we need a greater understanding of the ecology of these systems.

- Global warming is liable to affect freshwater ecosystems in New Zealand to varying degrees (MfE 2001, 2000). Potentially, greater extremes of precipitation and drought in different areas of the country will alter hydrological regimes in braided rivers already subjected to water abstraction and flow modification. Studies are needed to determine the likely consequences of global warming and climate change on our braided river ecosystems.
- New Zealand has more relatively un-impacted braided river systems than many other developed nations. Thus, we have an opportunity to contribute towards a greater global understanding of the ecological structure and function of these dynamic river systems.

9.0 Conclusion

Studies of spatial diversity patterns in the braided upper Waimakariri River by Gray et al. (2006) suggested that invertebrate communities reflect the high heterogeneity of floodplain habitats. In contrast to the restricted traditional view of braided rivers as species-depauperate, 'ecological deserts', these rivers and their floodplain reaches in fact represent spatially complex, temporally dynamic habitats with high landscape- and reach-scale biodiversity values. Living within and around this mosaic of aquatic habitats are a range of, often rare and little understood flora and fauna. A range of spatio-temporal factors appear to be important in regulating braided river invertebrate communities. In order to identify the specific influences of these various factors it is necessary to consider the river at the reach scale where individual floodplain habitats may be important, and from a holistic perspective where the river catchment is viewed in its entirety.

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Appendix 1. Studies included in the analysis of braided river main channel invertebrate communities.

Author(s)	Source of Flow	River	Country	Season	Sampler mesh size μm	Taxonomic richness		Mean Abundance (individuals/m^2)
(Hirsch 1958)	Alpine	Lower Waimakariri	NZ	winter + autumn		10	total	796
(Sagar 1986)	Alpine	Lower Rakaia	NZ	winter + autumn	530	33	total	1289
(Sagar and Eldon 1983)	Alpine	Lower Rakaia	NZ	winter + summer	530	22	total	2117
(Matthaei and Townsend 2000a)	Foot hill	Kye Burn	NZ	spring	250	13	mean	4855
(Fowler 2004)	Foot hill	Tukituki and Waipawa Rivers	NZ	summer	300	26	total	5500
(Fowler and Scarsbrook 2002)	Foot hill	Makaretu River	NZ	autumn	300	11	mean	2600
(Scrimgeour et al. 1988)	Foot hill	Ashley River	NZ	winter + spring	250	21	max	4070
(Matthaei et al. 2000)	Foot hill	Kye Burn	NZ	summer	250	12	mean	533
(Scarsbrook and Townsend 1993)	Foot hill	Timber Creek	NZ		300	16	mean	5330
(Fowler and Death 2000)	Foot hill	Waipawa River	NZ		300	10.4	mean	400
(Winterbourn et al. 1971)	Alpine	Waimakariri	NZ	summer	500	8	max	480
(Sagar and Eldon 1983)	Alpine	Rakaia River	NZ	all year	500	18	max	1798

(Sagar and Glova 1992)	Alpine	Rakaia River	NZ	all year	350	25	total	1630
(Pierce 1979)	Alpine	Cass River	NZ	all year	500	13	total	774
(Pierce 1983)	Alpine	Rakaia River	NZ	all year	500	5		101
	Foot							
(Death 1991)	hill	Kowai River	NZ	all year	250	62	total	
(Death 1991)	Alpine	Bruce Stream	NZ	all year	250	42	total	
(Scrimgeour and Winterbourn	Foot							
1989)	hill	Ashley River	NZ	all year	250	60		11 000
(Digby 1999)	Alpine	Rakaia River	NZ		200	39		
(Burgherr et al. 2002)	Alpine	Roseg River	Switzerland	all year	100			7575
(Brunke 2002)	Alpine	Brenno River	Switzerland		300	34	max	
(Brunke 2002)	Alpine	Lesgiuna River	Switzerland		300	24	max	
(Ward et al. 1999a)	Alpine	Roseg River	Switzerland					22 840
(Arscott et al. 2003)	Alpine	Tagliamento River	Italy	all year	100	51	mean	165 758
(Arscott et al. 2005)	Alpine	Tagliamento River	Italy		100	63	mean	40 543

Appendix 2. Studies included in the analysis of braided river spring invertebrate communities.

Author(s)	Catchment	Country	Season	Mesh size μm	Total taxa found	Abundance (individuals/m^2)
(Boud et al. 1959)	Glenariffe	NZ	summer			2618
(Barquin 2004)	Hawdon valley	NZ	summer	250	50	750
(Barquin 2004)	Hawdon valley	NZ		250	75	7000
(Digby 1999)	Rakaia River	NZ				
(Death 1991)	Waimakariri basin	NZ		250	45	11 000
(Gray 2005)	Waimakariri basin	NZ	all year	250	79	
(Gray *et al* 2006.)	Waimakariri basin	NZ	all year	251	81	
(Burgherr et al. 2002)	Roseg River	Switzerland				10 000
(Ward et al. 1999a)	Roseg River	Switzerland				76 430
(Arscott et al. 2005)	Tagliamento River	Italy		100	29	15 377
(Laperriere 1994)	Gerstle, Tanana and Delta Rivers	Alaska		1000	14	1000
(Hoffsten and Malmqvist 2000)	Various	Sweden	summer and autumn	500	16	
(Kownacki 1985)	Various	Azerbaijan			25	
(Zollhoefer et al. 2000)	Various	Switzerland		600	81	

Chapter 2. Braided river benthic diversity at multiple spatial scales: a hierarchical analysis of ß diversity in complex floodplain systems

The headwaters of the Waimakariri River, Canterbury, South Island (top) and the Waiapu River, East Cape, North Island.

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Abstract

Despite the occurrence of braided rivers globally and the frequency of their anthropogenic modification, the benthic diversity of their floodplains and in particular lateral and longitudinal patterns in their communities have been long ignored. Therefore, we conducted a spatially nested, hierarchical survey of 11 braided rivers in the South and North Islands of New Zealand to investigate benthic invertebrate diversity at multiple spatial scales. In each river 6 reaches and up to 5 floodplain habitat types within each reach were sampled. From a total of 203 sites we identified 145 taxa. Benthic invertebrate diversity was highly variable at the island, river, reach and habitat-scales. Diversity differences between islands were driven by high regional endemism. Diversity at the whole river-scale ranged from 99 taxa in the Wairau River to only 56 in the Waiapu River. At the reach-scale no significant differences in diversity or abundance were found longitudinally down the rivers. At the habitat-scale, lateral floodplain habitats, particularly spring creeks, consistently contained greater richness and abundance than adjacent main channel habitats. Comparisons of Whittaker's multiplicative Beta at different spatial scales revealed the greatest range and mean value of taxon turnover to be between habitats, within reaches. Additive partitioning of beta diversity indicated that diversity values at the broad spatial scales of reach and river, contributed disproportionately to overall diversity. Our results indicate that river managers concerned with maintaining diversity need to scale their efforts at the whole river scale rather than attempting management of smaller units representing local-scales. However, at finer scales, lateral floodplain habitats (particularly springs and floodplain ponds) are hotspots of diversity, and protection and remediation of these habitats is particularly important.

Introduction

Braided rivers are among the most dynamic and complex of all riverine systems (Ward et al. 2002). They are the products of high-energy environments where variable discharge regimes and heavy sediment loads interact to produce dynamic riverscapes (Bristow & Best 1993). Braided rivers typically have extensive flood plains, which are hydrologically connected to the river (Brunke & Gonser 1997, Ward et al. 1999, Woessner 2000), are spatially and temporally variable in groundwater–surface water exchanges (Stanford & Ward 1993, Brunke & Gonser 1997, Poole et al. 2002), and have a diverse array of habitats that are in a state of continual successional change (Arscott et al. 2000, van der Nat et al. 2003a). These conditions create a complex 3-dimensional mosaic of heterogeneous habitats along the river and across the floodplain with important consequences for spatial patterns of benthic invertebrate biodiversity (Ward et al. 2002).

Historically, stream ecologists have viewed braided river channels as unstable ecosystems (Percival 1932), with communities characterized by low species diversity (Sagar 1986), and dominated by a few "weedy" species (Scrimgeour & Winterbourn 1989). However, a more holistic view of the "river", which includes lateral habitats of the wider floodplain and underlying groundwaters, in addition to the main braids, has revealed that braided reaches represent hotspots of biodiversity within the greater riverscape (Stanford 1998, Ward et al. 1999, Arscott et al 2005, Karaus et al. 2005, Gray et al. 2006).

Braided rivers are common in erosion prone areas of the world and whereas the head waters of many of these rivers may remain relatively free from human modification their lower reaches include some of the most severely modified river systems on the planet. In most developed regions few examples of unmodified braided floodplain systems remain (Ward et al. 1999). Internationally, both the surface waters and groundwaters associated with braided rivers have been targeted by irrigators and municipal water suppliers (Pringle 2001, Hancock 2002, Malmqvist & Rundle 2002, Young et al. 2004) and many major rivers have been impounded for the generation of hydro-electricity (Nilsson et al. 2005). The negative impact of flow regulation on the morphological and successional

diversity of braided river floodplain habitats has been highlighted by several workers (Ward & Stanford 1995, Gilvear 2004, Hauer & Lorang 2004, Hohensinner et al. 2004). Flow alterations typically reduce channel-forming flows and longitudinal sediment transport, which in turn reduce the rate of channel migration, and habitat turnover. The effect of flow regulation truncates the fluvial system and disconnects the river from its floodplain (Hohensinner et al. 2004). These modifications are generally assumed to have deleterious effects on invertebrate diversity in floodplain river systems, although this has rarely been assessed directly (Karaus 2004).

Due to the multiplicative array of pressures acting upon braided river ecosystems there is an urgent need for baseline ecological data. Species are distributed heterogeneously among habitats, landscapes and regions and an understanding of how patterns in taxon occurrence vary across space and spatial scales is essential to preserve extant diversity. For example, controversy over the optimal size or design of nature reserves is primarily driven by a failure to account for scaling differences between organisms (Wiens 1989). Hierarchy theory (Allen & Starr 1982, O'Neil et al. 1986) may provide some insights into spatial variation in diversity in lotic systems (Frissell 1986, Poff 1997) in particularly braided river floodplains (Poole 2002, Thorp et al. 2006). Ward et al. (1999) developed a hierarchical framework to apply the concept of beta diversity to floodplain rivers. The concept of beta diversity in an ecological context was introduced by Whittaker (1960) to quantify changes in taxon composition and abundance across environmental gradients. Gamma diversity (the regional taxa pool) is a function of the number of taxa in each habitat type (alpha diversity) and the turnover of taxa between habitats (beta diversity). Ward & Tockner (2001) suggested that the identification of significant hierarchical levels or domains might help identify factors that constrain or generate biodiversity. Their framework employed Whittaker's multiplicative beta ($\gamma = \alpha \times \beta$). Recently, the revival of a parallel calculation of beta, the additive relationship ($\gamma = \alpha + \beta$), has enabled the partitioning and direct comparison of diversity across multiple spatial scales (Lande 1996, Veech et al. 2002). Additive partitions have been applied to stream benthic invertebrates (Allan 1975, Stendera & Johnson 2005), plants in agricultural fields

(Wagner et al. 2000), arboreal beetles (Gering et al. 2003), and across three variably impacted floodplain rivers in Europe (Karaus 2004).

Resource and conservation managers are in need of guidance as to the most efficacious use of their resources for the preservation of extant diversity in braided river systems. For example, are the diversity and communities of all braided rivers in a country the same? Within a river, are there predictable reaches which are of greater ecological value? Similarly, are particular habitats within braided rivers of greater relative importance to overall system biodiversity? In order to address these questions we investigated the spatial distribution of braided river invertebrate diversity by both multiplicative and additive beta analysis, at five spatial scales, New Zealand, North and South Island, river, reach and floodplain habitat and discuss the implications of the spatial configurations found to conservation and resource management.

Methods

Study area

New Zealand is a mountainous country with over half its surface comprising steep, valley-dissected terrain. The alpine spine of New Zealand is aligned perpendicular to the prevailing westerly airflow. Consequently, frequent, extreme and unpredictable orographic precipitation defines the hydrology of New Zealand's rivers and streams. Furthermore, sediment yields for some West Coast rivers are amongst the highest recorded in the world (Griffiths 1979). Braided rivers are a product of these climatic and topographical conditions, which along with the relatively low levels of anthropogenic impacts have bequeathed New Zealand with over 163 rivers having braided reaches that comprise 248, 000 ha of floodplain habitat (Wilson 2001).

Site selection, characteristics and sampling procedure

Eleven rivers were sampled, three in the North Island and eight in the South Island, distributed in accordance with the abundance of braided rivers within New Zealand (Wilson 2001) (Fig. 1a). The rivers ranged in mean discharge from 44 m^3 s^{-1} (Waiapu River) to 370 m^3 s^{-1} (Waitaki River) (Table 1), and catchment area ranged from 998 km^2

(Taramakau River) to 11, 887 km^2 (Waitaki River). Rivers were further characterized according to hydrology, climate and vegetation cover categories, which were derived from the Freshwater Environments of New Zealand (FWENZ) database (Wild et al. 2005) and the River Environment Classification (REC) (Snelder et al. 2005). The Waitaki River is highly modified in its lower reaches by a series of impoundments, therefore for the sake of characterization, the river was considered to comprise separate entities above and below the dams (Table 1). Rivers were characterized hydrologically using the average number of floods per year that exceeded three times the median flow of the river (FRE3), a criterion that is ecologically relevant to stream biota (Clausen & Biggs 1997). Values ranged from an average of 24 events per year in the Landsborough River to 0.6 in the regulated lower Waitaki River. FRE3 values were generally lower for North Island rivers than South Island rivers, which have more alpine catchments. Rainfall days per year were highest in rivers on the West Coast of the South Island, e.g., the Landsborough and Taramakau rivers, and lowest in the Oreti River in the south of the South Island. In general, South Island rivers experienced more rain days per year than those in the North Island. Predominant catchment vegetation cover in the North Island was pasture. However, in South Island rivers the northern and western regions were dominated by indigenous forest, whereas east coast rivers were mainly covered by scrub and bare ground.

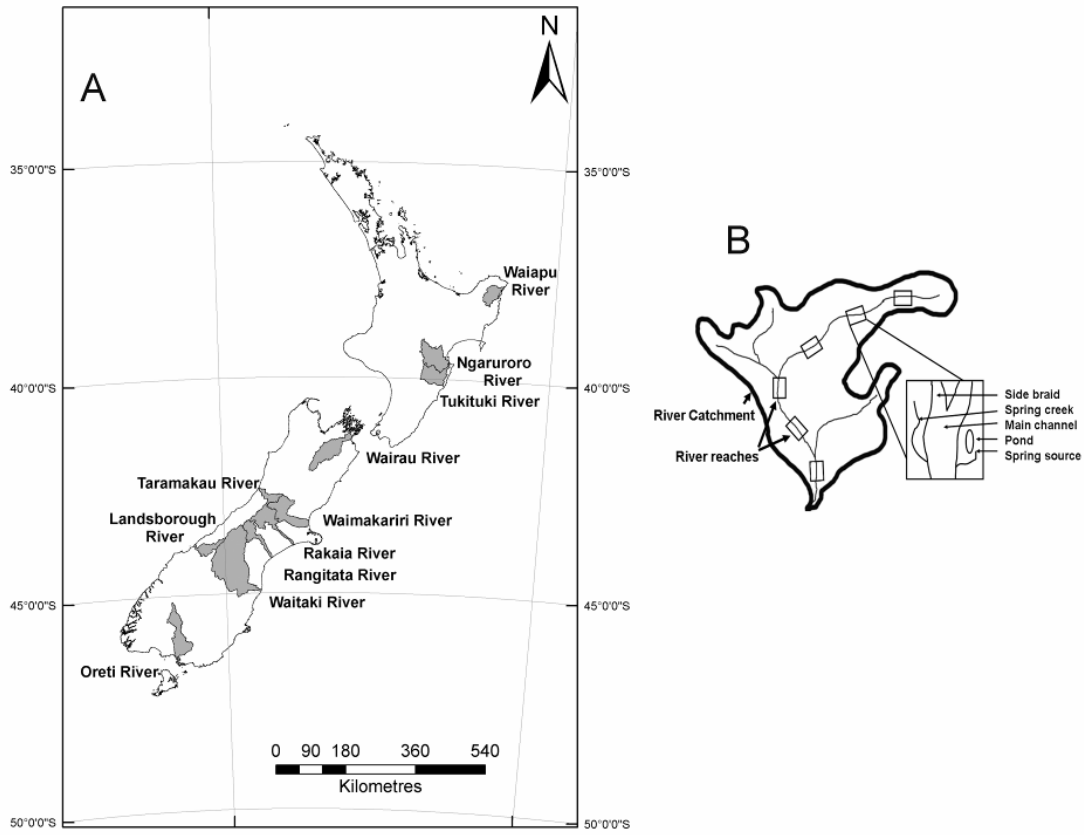

Figure 1 A). Eleven braided river catchments included in the survey, three in the North Island and 8 in the South Island B) Up to six reaches were sampled within each catchment and five floodplain habitats in each reach.

Six reaches, approximately 1 km long, were selected at intervals along each river (Fig. 1b). The uppermost reach was in the steeper headwaters, above the point where a distinct floodplain first appears on a 1: 50,000 topographical map. In these reaches the river was generally 3rd-4th order (Strahler 1957). The lowest reach was close to the river mouth, beyond estuarine and brackish water zones and above tidal influence. Intermediate reaches were distributed evenly between the uppermost and lowermost reaches. Where present, a gorge reach was included. Anthropogenic impacts generally increased downstream although there was considerable variation among rivers.

Table 1. Catchment characteristics of the 11 braided rivers considered in our study. Rivers are ordered north to south, and rivers 1 to 3 are on the North Island. The FRE3 value represents the annual frequency of flows >3× the median flow (Clausen and Biggs 1997).

Catchment	Region	Catchment area (km^2)	River order[a]	Mean discharge (m^3/s)[b]	FRE 3 excedence	Rain d/y[b]	Catchment vegetation[c]
Waiapu	East Cape	1574	6	82	7.1	19.3	Pasture
Ngaruroro	Hawkes Bay	2009	6	46	10.4	10	Pasture
Tukituki	Hawkes Bay	2495	6	44	10	7.98	Pasture
Wairau	Nelson-Marlborough	3574	7	99	11.5	13.3	Indigenous forest
Taramakau	West Coast	998	6	150	22.6	64.7	Indigenous forest
Waimakariri	Canterbury	3541	7	128	15.3	17.2	Scrub/tussock
Rakaia	Canterbury	2830	7	175	14.3	24.1	Bare ground
Rangitata	Canterbury	1809	6	109	10.9	26.2	Bare ground
Landsborough	West Coast	1341	6	277	24	81.7	Indigenous forest
Waitaki (upper)	Canterbury	11,887	7	370	9.4	52.1	Bare ground
Waitaki (lower)	Canterbury				0.6	14.1	Scrub/tussock
Oreti	Southland	3513	7	62	13.4	4.9	Pasture

[a] River order (Strahler 1957)

[b] Variables derived from Freshwater Environments of New Zealand (FWENZ; Wild et al. 2005) database correspond to the lowest segment of each river system

[c] Catchment vegetation assigns rivers to 7 categories representing the predominant land-cover of the catchment (from River Environment Classification; Snelder et al. 2005).

A single transect located at the approximate mid-point of each reach was established across the entire floodplain. Transects were approximately straight and perpendicular to the main channel. All habitats visible from the transect line were assessed and the most successionally mature example of each of five habitat types when present, was sampled (Fig. 1b). Habitat types were the main channel, a side braid or secondary channel (with upstream and downstream connection to the main channel), a floodplain pond, a spring

source and a spring creek, located at least 50 m downstream from the source of another spring-fed stream.

Biological samples were collected during baseflow conditions between December 2006 and April 2007 and consisted of 3 Surber samples (0.11 m^2, mesh size 250 μm) and a single extensive kick-net (mesh size 250 μm) sample (using the Protocol described in Stark et al. 2001). Kick-netting was performed for 5 minutes over an approximately 3 m^2 area within each habitat. Quantitative pond samples were taken using a modified Surber sampler (0.11 m^2, mesh size 250 μm), where the sampling quadrat was completely enclosed by mesh and invertebrates were washed and agitated into the net by hand.

Samples were preserved in 70% ethanol in the field, concentrated on a 250 μm mesh sieve in the laboratory and sorted under 40 x magnification. Identifications were made to the lowest taxonomic level possible, except for Oligochaeta, which were not differentiated below order and Chironomidae, which were not separated below tribe. Identifications were made using the keys and guides of Winterbourn (1973), Chapman & Lewis (1976), Cowley (1978), McLellan (1991, 1998), Winterbourn et al. (2000), Smith (2001), Scarsbrook et al. (2003) and a description by Percival (1945).

Analysis

For each habitat invertebrate data from the 3 Surber samples were summed, and for every new taxon found only in the kick-net sample, a single individual was added to the combined taxon list. All subsequent analyses of diversity were performed on this dataset, however species accumulation curves and comparisons of abundance used quantitative data only. Differences between taxon richness and abundance in habitats and reaches were assessed in Systat (2000) using ANOVA and Bonferroni *post hoc* tests. Log transformations were made when necessary after checking data for normality and residuals for homogeneity of variance.

Species accumulation curves were used to estimate the efficiency of sampling effort at different spatial scales. A species accumulation curve displays the number of observed

species as a function of sampling effort (usually samples or individuals). Theoretically, the curve will reach an asymptote when no further increase in sampling effort returns any new species. Taxon accumulation curves were produced using EstimateS (Colwell 2005).

Whittaker's multiplicative beta, regional richness = alpha x beta, (Whittaker 1960) has traditionally been used to quantify rates of change along an environmental gradient (Veech et al. 2002, Magurran 2004), although its use has been criticized. Specifically, Vellend (2001) showed that Whittaker's beta and its derivatives are independent of the distributions of taxa on spatial or environmental gradients, and therefore that beta does not reflect "true species turnover" along a gradient. However, in the context of our study, where spatial gradients are of secondary interest to underlying taxon heterogeneity, use of a multiplicative suite of beta measures is appropriate. Harrison et al. (1992) modified Whittaker's original formula for beta diversity to remove the effect of variable alpha levels, which influence patterns in beta. We therefore adopted their measure to remove the variation in alpha caused by variable sampling effort at each hierarchical level. Thus, Whittaker's beta 2:

$$(S/\alpha_{max}) - 1/(N - 1) \times 100$$

where S is richness within the scale of interest + 1 and α_{max} is the maximum value of alpha diversity in the collection of N habitats/reaches/rivers etc. at that scale. This variation of beta measures the amount by which richness at any one spatial scale exceeds the maximum richness of any spatial units nested within it. Values range from 0 to 100, with 0 representing identical diversity and 100 representing total dissimilarity.

The traditional multiplicative beta indices produce values of alpha and beta that are not directly commensurate and therefore cannot be directly compared (Veech et al. 2002). When using richness values, taxa are the units of alpha, but beta is unit-less. Furthermore, when using the multiplicative relationship, diversity components are not weighted equally when applied to more than one spatial scale (Gering & Crist 2002). However, the total taxon richness in a pooled set of communities/samples/spatial units can also be

partitioned into additive components within and among those groups such that total richness and its components have the same units and can be compared directly, e.g., regional richness = alpha + beta, (Lande 1996, Crist et al. 2003). Thus, additive partitions can be used to directly compare the contributions across spatial or temporal sampling scales to total richness (Allan 1975, Wagner et al. 2000, Devries & Walla 2001, Fournier & Loreau 2001, Gering et al. 2003, Stendera & Johnson 2005, Ribeiro et al. 2008).

Although the multiplicative suit and additive methods of calculating alpha, beta and gamma are mathematically related measures of diversity (Kiflawi & Spencer 2004; Ricotta 2005), our use of these indices describes different aspects of spatial diversity. Our presentation of Whittaker's relationship was calculated separately at each spatial scale using richness values. Whittaker's relationship in this context describes heterogeneity in richness values between all habitat units within a spatial scale. The calculation of additive diversity uses abundance data and incorporates all spatial scales and individuals in a single analysis. It essentially describes the greatest spatial scale at which taxa are unique, and hence, which scale contributes most to overall diversity.

Until recently, the use of additive partitioning was primarily descriptive and statistical methods for testing null hypotheses were lacking. However, the development of an empirical approach, based on randomisation, permits a more rigorous evaluation of the arrangement of diversity components across scales (Crist et al. 2003). We used individual based randomization using the software package PARTITION (Crist et al. 2003) to assess the significance of components. The numbers of individuals and taxa in samples are determined by the random replacement of individuals at the lowest level, whilst preserving the original species abundance and sample-size distributions. This process was repeated 10,000 times and each randomised data set was then partitioned into its additive components. The probability (*p* value) that a diversity component greater or less than the observed value could have been obtained by chance is obtained from the proportion of null values that are greater or less than the observed value (Crist et al. 2003).

PARTITION calculates the additive components of diversity using taxonomic richness, Shannon and Simpson diversity. As a heterogeneity measure the Shannon index emphasises taxon richness, but takes into account the degree of evenness in species abundances, such that greater values are obtained when the abundances of separate species are equal. In contrast, Simpson's index is a dominance measure weighted towards the abundances of the most common taxa rather than the number of different taxa (Magurran 2004). Taxa were defined as rare or common based on their proportional abundance throughout the entire study (Gering et al. 2003). Rare taxa represented < 0.05 % of the total number of individuals collected and common taxa represented > 0.05 % of individuals. Diversity partitions were performed on all, rare and common taxa.

Results

We identified 145 taxa from a total of 203 sites using the combined quantitative and qualitative data set; 61 were common taxa and 84 were rare. The majority of individuals (63%) belonged to 5 taxa, of which the leptophlebiid mayfly, *Deleatidium* and Orthocladiinae (Chironomidae) comprised 44% of all individuals. Chironominae, the gastropod *Potamopyrgus antipodarum* and Elmidae (Coleoptera) complete the list of five most common taxa overall. Of the 145 taxa, 37 (25%) were unique to the South Island and 9 (6%) were only found in the North Island. Twenty-six taxa were represented by 5 or fewer individuals, including some taxa represented by single individuals. Singleton taxa were Trichoptera (3), Plecoptera (1), Odonata (1), Diptera (2) and Coleoptera (1).

River-scale

Taxonomic richness ranged from 56 taxa in the Waiapu River to 99 taxa in the Wairau River, and represented 38% and 68% of the entire taxa pool, respectively (Fig. 2a). The 5 rivers with the highest taxonomic richness were in 5 separate geographic regions. All ordinal groups were represented in each river system with the exception of Plecoptera, which were absent from the Waiapu River. Most rivers were dominated by trichopteran taxa, except the Landsborough and Waiapu rivers, which contained a greater number of dipteran taxa. The proportions of ordinal groups were similar among rivers despite considerable variation in overall richness. Total number of individuals ranged from

approximately 19, 500 in the Wairau and Ngaruroro rivers, to fewer than 3500 individuals in the Landsborough and Waiapu rivers (Fig. 2b). In terms of relative abundance of individuals all rivers were dominated by Diptera, except the Ngaruroro, Rakaia and Waitaki, which contained proportionally more mayflies. The Waitaki River was unusual in having a high proportion of Crustacea (17%), predominantly the amphipod *Paracalliope fluviatilis*, which dominated the impounded lower reaches. This amphipod is normally associated with stable, weedy streams (Chapman & Lewis 1976), but was abundant in the main channel of this modified river.

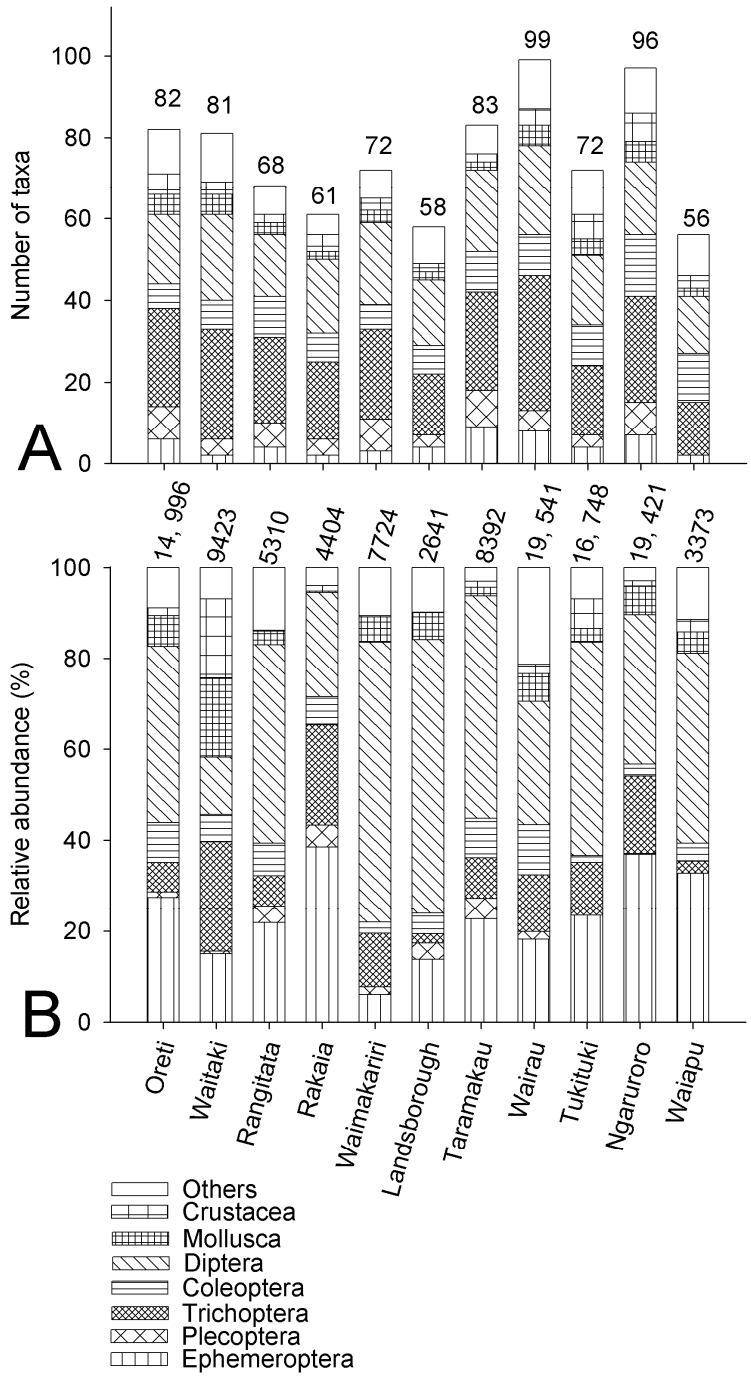

Figure 2 A) Taxonomic richness of ordinal (or higher) groups for rivers sampled during austral summer between December 2006 and April 2007. Total taxonomic richness is shown above each bar, B) relative abundance of ordinal (or higher) groups collected in each river. Total number of individuals is shown above each bar.

Reach-scale

Taxonomic richness and density did not differ significantly along the river systems (Fig. 3a & b). However, both metrics were highly variable both within and across individual rivers.

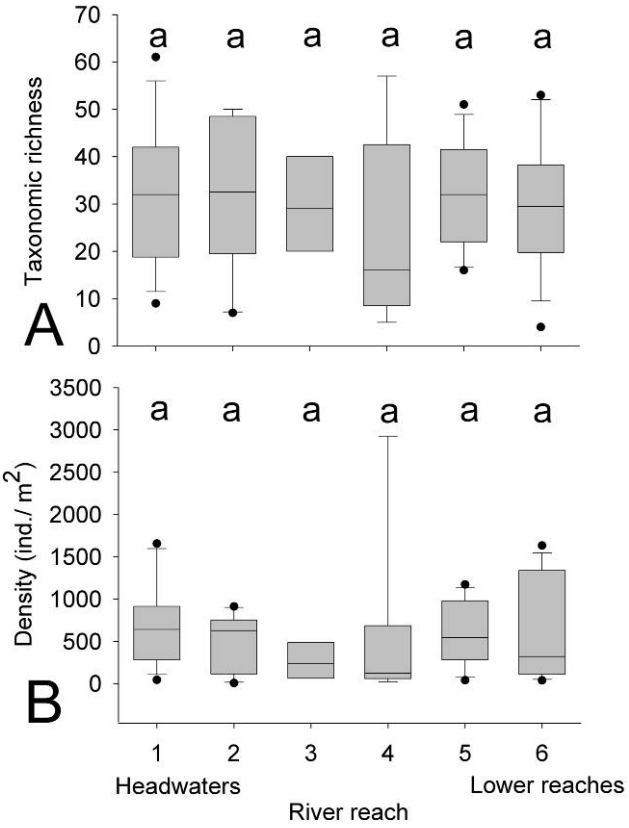

Figure 3. Reach-scale (A) taxonomic richness and, (B) density (median, 25th and 75th percentiles, and outliers). Values with the same letter above the plot are not significantly different (Bonferroni post-hoc test, $p>0.05$). Taxonomic richness d.f. $_{5, 60}$, F = 0.485, p = 0.787. Average density (m^2), d.f. $_{5, 60}$, F= 0.407, p = 0.842.

Habitat- scale

Richness and density varied significantly among habitat types (Fig. 4a & b). Thus, spring sources, spring creeks and ponds had greater richness than main channels, whereas side braids had intermediate diversity. Spring creeks had the highest mean taxonomic richness. Ponds and spring creeks had significantly higher densities than main channels and side braids.

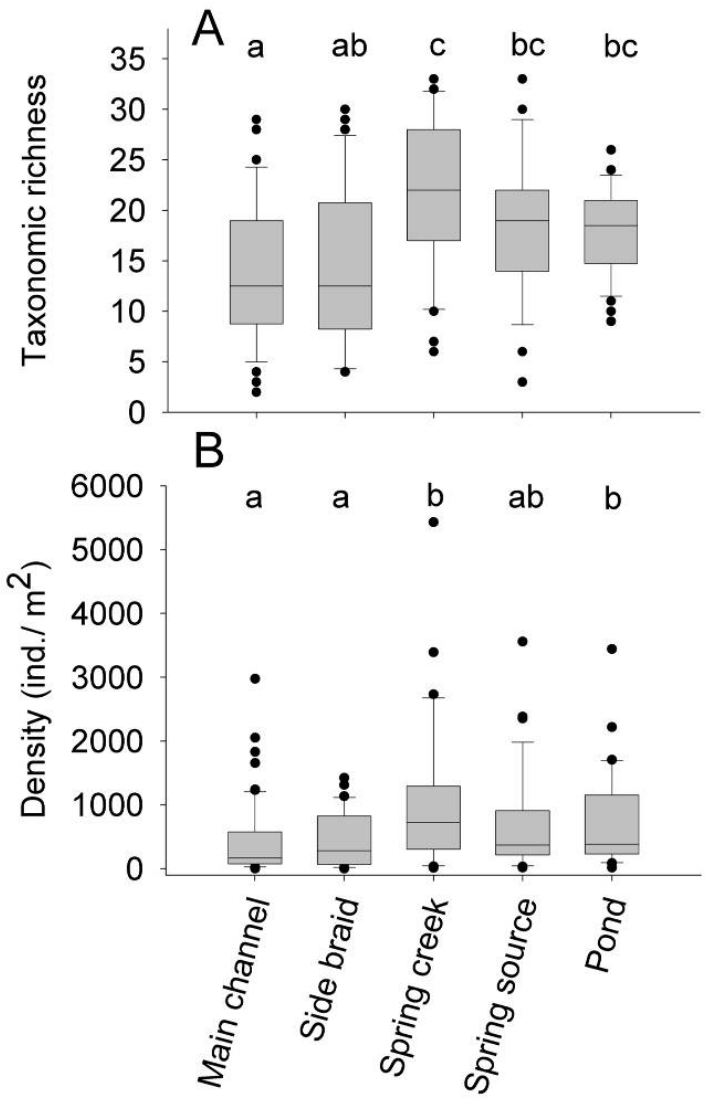

Figure 4. Floodplain habitat-scale analysis of A) taxonomic richness and, (B) invertebrate density (median, 25th and 75th percentiles, and outliers) in five habitat types sampled across six reaches of eleven braided rivers. Values with the same letter above the plot are not significantly different (Bonferroni post-hoc test, P>0.05). Density was log transformed to meet assumptions of normality required by a parametric ANOVA test, but actual values are shown on the plot. Taxonomic richness, $d.f._{4, 196}$, $F = 9.743$, $p < 0.001$. Density, $d.f._{4, 196}$, $F = 5.114$, $p = 0.001$.

We calculated the proportional richness of each lateral habitat relative to its associated main channel and then ranked sites within each habitat type for clearer presentation (Fig. 5a). Sites with a proportional richness >1 contained more taxa than the adjacent main

channel. Over 70% of lateral floodplain habitats had greater invertebrate richness than their associated main channel. All spring creeks (except 1) had more taxa than their associated main channel, but ponds, spring sources and side braids were more variable in relative taxonomic richness with 74%, 76%, and 75% of sites, respectively having a higher diversity than the main channel. Three ponds had over 4 times as many taxa as the nearby main channel. Taxonomic richness in lateral habitats never fell below half the richness found in the main channel, suggesting that main channels may represent the lower limit for floodplain diversity in braided rivers.

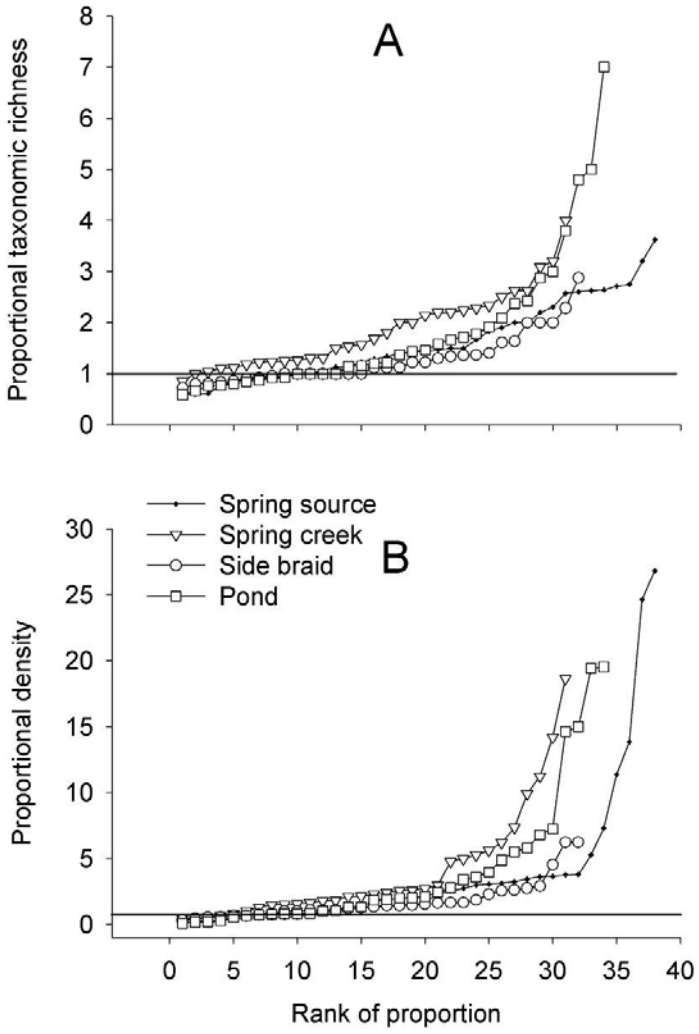

Figure 5. Comparisons of benthic invertebrate A) taxonomic richness and, (B) density in lateral floodplain habitats relative to their associated main channel. Each point in A represents the total from three Surber samples and a kick-net, whereas density was calculated using summed surber data only. Proportions have been ranked within each habitat type for clearer presentation.

Of the lateral habitats, 73% contained a higher density of invertebrates than their associated main channel (Fig. 5b). Specifically, 84% of spring creeks, 66% of spring sources, 68% of ponds and 75% of side braids had higher densities of individuals than the main channel.

Sampling efficiency

Taxon accumulation curves for individual rivers did not reach an asymptote, indicating that our sampling within rivers was unlikely to have encompassed their full taxonomic diversity (Fig. 6). In contrast, the accumulation curve for the South Island approached an asymptote indicating that the 151 samples from 8 rivers provided a strong estimate of total taxonomic richness. The North Island curve (3 rivers) followed a similar trajectory as did that for the full survey of 11 rivers.

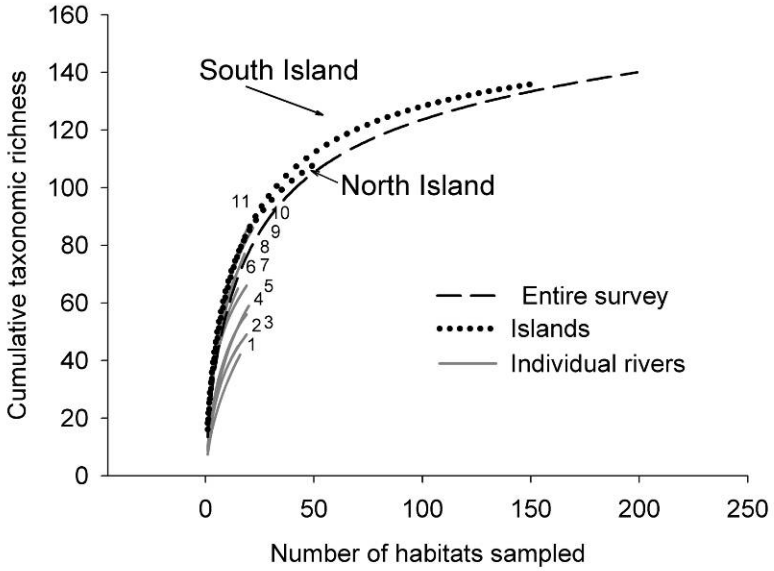

Figure 6. Taxonomic richness accumulations curves from 201 braided river habitats, sampled across eleven rivers, two islands (North and South Islands) and all data combined. Rivers are 1. Landsborough, 2. Waiapu, 3. Rakaia, 4. Rangitata, 5. Waimakariri, 6. Tukituki, 7. Waitaki, 8. Oreti, 9. Taramakau, 10. Wairau, 11. Ngaruroro.

Whittaker's beta diversity

The richness (alpha) of hierarchical units increased with increasing spatial scale, i.e., at higher levels of the hierarchy (Fig. 7). The range and variability of taxonomic turnover (beta 2) also varied across spatial scales (Fig. 7) and was highest between floodplain habitats at the reach-scale. This indicated that floodplain habitats were more different from each other in taxonomic richness than units at higher levels of the hierarchy. Taxonomic turnover between islands was marginally higher than mean turnover within an island and reflected the high number of taxa endemic to each island. Thus, of the 145 taxa 25% were unique to the South Island and 6% were only found in the North Island.

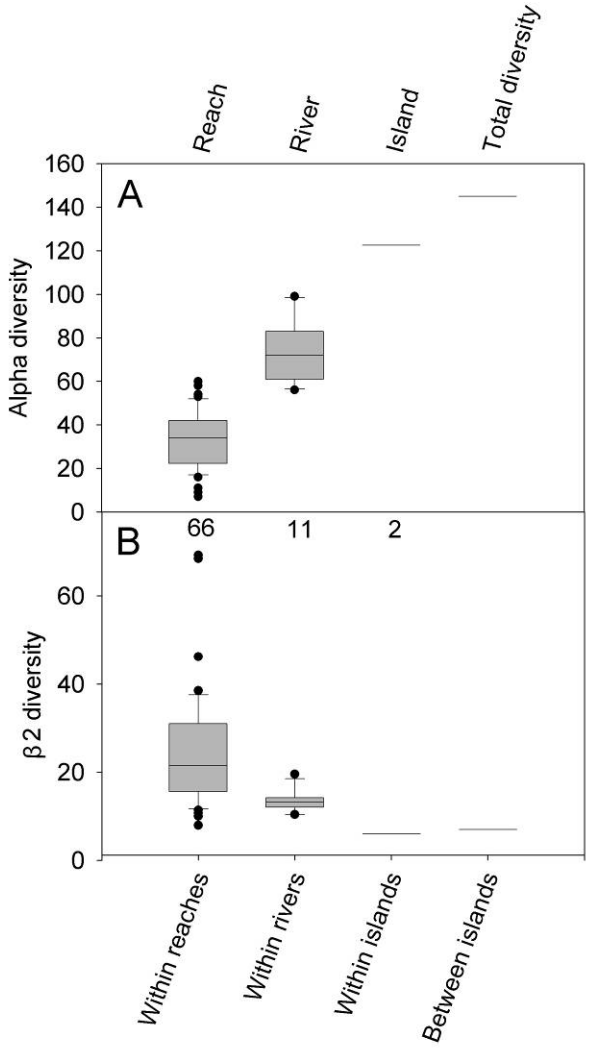

Figure 7. Alpha richness and Whittaker's beta 2 across four spatial scales. The number of beta calculations at each scale is marked along the midline of the graph.

Additive diversity partitioning

These patterns were evident across all taxa groups and indices despite the alpha component of common taxa being a substantial proportion (28 %) of overall diversity (Fig. 8) and a large proportion of the Shannon (54 %) and Simpson (74 %) diversity (Fig. 9).

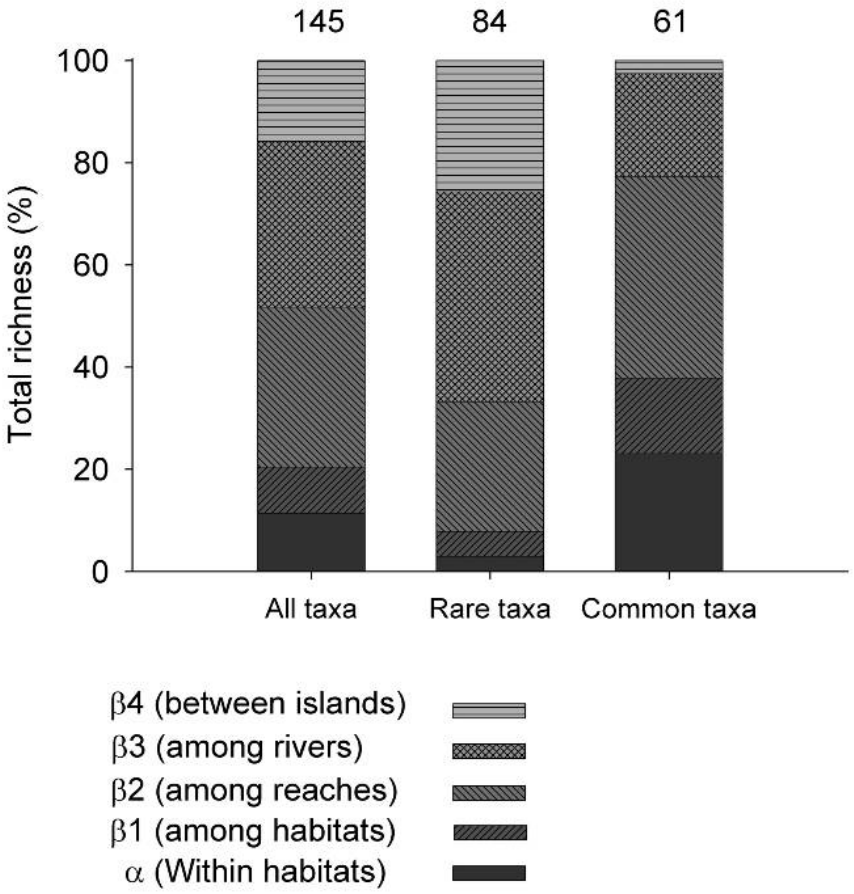

Figure 8. Percentage of total benthic invertebrate richness explained by alpha and beta at four different spatial scales: among islands, among rivers, among reaches, among and within habitats. The contribution of each spatial scale to total richness was determined by additive partitioning. The total number of taxa are shown above each bar.

Higher values of Shannon's index are obtained when both richness and evenness are high, whereas Simpson's index is weighted towards the abundance of dominant taxa (Fig. 9). The differences between alpha values for richness, Shannon's and Simpson's indices are a measure of the extent to which communities are dominated by common taxa.

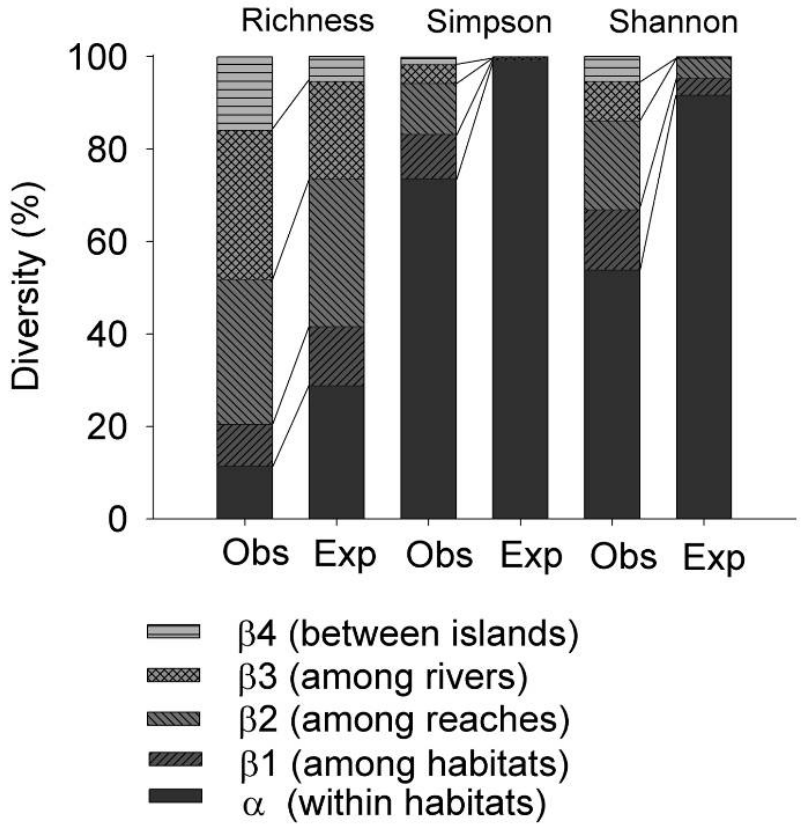

Figure 9. Percentage of total richness, Shannon and Simpson diversity explained by alpha and beta components of richness at four spatial scales: islands, rivers, reaches and habitats. Observed and expected components were calculated by additive partitioning of diversity. Expected components were based on the distributions of 10,000 individual based randomizations.

We also found differences in the relative proportions and significance of diversity values between all taxa, rare taxa and common taxa across the hierarchical model (Fig. 8). For the entire community the observed beta 2 (turnover amongst reaches) was not significantly different from the expected proportion derived from randomization (Table 2). However, for rare taxa beta 2 was less than expected and for common taxa it was greater than expected (Table 2). The result for rare taxa suggests that between reaches within rivers there is little turnover of rare taxa. In contrast, turnover of common taxa was greater than expected suggesting that communities varied significantly among reaches in terms of composition. Diversity amongst all taxa was spread relatively equitably

between beta 2 and 3, whereas for rare taxa it was allocated to beta 3 and for common taxa, beta 2 (Fig. 8).

Table 2. Significance tests of observed diversity estimates against null estimates derived from 10,000 additive partition randomizations. Values were partitioned among islands (β4), rivers (β3), reaches (β2), and habitats (β1), and within habitats (α). Significance was determined at the 0.05 level. + = diversity greater than expected, – = diversity lower than expected, ns = not significant. Simpson and Shannon diversity were not tested for common and rare taxa only.

Group	Level	Richness	Simpson	Shannon
Entire community	β4	+	+	+
	β3	+	+	+
	β2	ns	+	+
	β1	–	+	+
	α	–	–	–
Rare taxa	β4	+		
	β3	+		
	β2	–		
	β1	–		
	α	–		
Common taxa	β4	+		
	β3	+		
	β2	+		
	β1	–		
	α	–		

Discussion

Braided rivers are regarded as hostile environments, which should therefore, be characterized by depauperate aquatic invertebrate communities (Percival 1932, Tockner et al. 2006). Studies performed in the main channel of braided rivers have shown communities dominated by a low number of "weedy" species that show refuge seeking behaviors, flexible life histories and rapid recolonisation mechanisms (Scrimgeour & Winterbourn 1989, Sagar & Glova 1992, Arscott et al. 2003 a & b). However, recent research incorporating lateral floodplain habitats has demonstrated the potentially high richness and productivity of these habitats within the greater riverscape (Karaus 2004,

Gray et al. 2006) and shows that floodplains may have high overall richness, which can be important regionally (Burgherr et al. 2002, Tockner & Stanford 2002). The high species richness of some braided river floodplains appears to be the result of high floodplain habitat heterogeneity maintained by a shifting habitat mosaic (SHM) driven by fluvial dynamics (Arscott et al. 2002, Van der Nat et al. 2003a). Floodplains maintain high hydrological connectivity between a 3-dimensional array of physically and successionally diverse aquatic habitats (Stanford 1998, Poole et al 2002, Ward et al 2002, Haur & Lorang 2004), however, consistency in patterns of diversity and abundance across multiple reaches, rivers and regions has not been considered, previously.

The 11 rivers in this survey showed marked variation in taxon richness, absolute and relative abundance of macroinvertebrates. The variation in taxon richness reflects to some degree the high level of regional endemism of New Zealand stream invertebrates (Harding et al. 1997, Boothroyd 2000). However, the primary influence on river community structure is more likely to be the physical characteristics of each river system (Winterbourn et al. 1981). Thus, the 11 rivers differed in terms of catchment-scale variables, such as mean discharge, flow regime, climate and vegetation characteristics. Although direct linkages are hard to quantify, numerous conceptual models and field based studies have indicated biological responses to catchment-scale variables (Poff 1997, Harding et al. 1998, Townsend et al. 2003, Death & Joy 2004, Townsend et al. 2004). In particular, antecedent flooding has a strong effect on invertebrate community structure in the main channels of braided rivers in New Zealand and Italy (Sagar 1986, Arscott et al. 2003b).

The braided river reaches included in our study showed no consistent longitudinal patterns in richness or density, which where highly variable both within and between reaches. This suggests that community structure (richness and abundance), rather than being a product of predictable changes along a river, may in fact be more strongly regulated by physico-chemical conditions at the reach-scale within those rivers. Similarly, in a study of Trichoptera diversity in two headwater floodplains Arscott (2003a) suggested that both habitat and the Trichoptera assemblage were dependent on

reach-scale factors that were uncoupled from position in the longitudinal continuum. Although a predictable downstream pattern in diversity may occur in a single channel river (Vannote et al. 1980), such a pattern is likely to be confounded in braided rivers due to the influence of discontinuities, such as gorges, alternating with physically diverse braided reaches, much like "beads on a string" (Stanford & Ward 1993, Ward & Stanford 1995). The reach-specific morphology of braided rivers has been linked to the degree of constriction by valley sides and the presence of protruding bluffs and tributary fans (Stanford & Ward 1993). Characteristics of floodplain vegetation have also been strongly implicated in influencing floodplain morphology, particularly channel form and diversity (Huang & Nanson 1997, Millar 2000, Gran & Paola 2001). Furthermore, large woody debris derived from eroded floodplain vegetation has been linked to habitat diversity within a river reach and tends to be more prominent in the headwaters, at least of the braided Tagliamento River, Italy (Gurnell et al. 2002, Van der Nat et al. 2003b).

Several previous studies have reported that groundwater-fed floodplain channels had higher invertebrate richness than main channels (McCabe 1998, Burgherr et al. 2002, Gray et al. 2006). These findings contrast with those of Arscott et al. (2005) who found that invertebrate richness within three groundwater-fed channels was lower than in the main channel of the Tagliamento River. In rivers where disturbance events are insufficiently intense or frequent to suppress taxonomic richness, such as many impounded rivers, main channel diversity values may attain similar or greater levels than those of lateral habitats (Karaus 2004). Low levels of disturbance may account for the relatively high invertebrate richness seen in some main channel habitats in our study. Conversely, some lateral habitats may have been recently disturbed resulting in diversity values that were similar to or lower than those in the adjacent main channel. Recolonisation of discrete lateral habitats such as ponds and springs may be slower than in the main channel as they lack up-stream colonists.

Our finding that Whittaker's beta values were greater within reaches than at any larger scale is indicative of the diversity of habitat conditions known to occur across the floodplains where strong gradients in environmental conditions are found between main

channels and lateral habitats (Arscott et al. 2000, 2001, Karaus et al. 2005, Tockner et al. 2006, Gray & Harding 2007). Consequently, different habitats support distinct assemblages of invertebrates, including taxa that are unique to them (Gray et al. 2006). The high level of turnover between habitats within reaches emphasises the importance of lateral habitats to overall braided river diversity.

Additive diversity partitioning showed that beta diversity was consistently greater at larger spatial scales, confirming that there were strong regional effects on the richness and composition of braided-river communities. As already mentioned, these differences may be partly due to regional endemism, but they may also be driven by catchment-scale physical characteristics of each river. The partitioning results for all taxa combined were similar to those for rare taxa, which suggested that rare species were driving patterns of the entire community. This is not surprising, as rare species accounted for 58% of all taxa found. The large number of rare taxa found in this study produced the relatively large, broad-scale, components of diversity in the partitions, as exemplified when rare taxa were removed for the common taxa analysis. These rare taxa were unique to the broadest scale of the analysis to which they were allocated.

Despite the sampling intensity of our study, the accumulation curves did not approach an asymptote at the reach or river-scale, and suggest we did not quantify the entire diversity of any river system. This finding has implications for the design of conservation inventories, which seek to produce a comprehensive list of taxa present in a region or system of interest. The best way to achieve such a goal is through intensive sampling of a limited area, although some rare taxa are still likely to be missed that would be found in a more spatially intensive survey (Gering et al. 2003). The disproportionate accumulation of rare taxa at broad spatial scales and the failure to saturate accumulation curves suggest that obtaining complete inventories is an unrealistic goal.

Contrasting patterns of diversity partitioning between taxon richness, Simpson's and Shannon's indices can be explained by patterns of taxon rarity and abundance as explained earlier. The contrast between partitioning of richness and dominance/evenness

illustrated the extent to which small spatial scales were dominated by common taxa, a finding consistent with existing knowledge of braided river communities, particularly the main channels of New Zealand rivers (Scrimgeour & Winterbourn 1989).

Implications for conservation management

Our findings have two major implications for the preservation of extant biodiversity in braided river systems. First, the disproportionate contribution of broad spatial scales to overall diversity, suggests that a focus on the large-scale is most appropriate for the retention of rare taxa. Overall diversity will be best protected by safeguarding whole reaches and catchments rather than attempts at management of local-scale habitats. This is particularly pertinent for braided rivers where many of the individual habitats in a reach are naturally transient or regularly disturbed (Reinfelds & Nanson 1993, Arscott 2002). Reach-scale management approaches must also be considered within a holistic framework because of the non-independence of reaches within a river system and because disturbances, such as impoundment, can be transmitted both up- and downstream (Ward & Stanford 1995, Pringle 1997). Thus, the basic conservation unit needs to be the river and its catchment. The spatial scales of importance for rare taxa (reach and river), also encompass the scales of relevance for common taxa (reach and habitat). Management targeting the diversity of rare taxa should therefore maintain the overall functionality of stream communities. However, this is almost certainly a false panacea, whilst we might aspire to preserve the entire diversity of an appropriate selection of rivers, the implications of the complete loss of functionality, the ecosystem services of invertebrate communities, in all unprotected streams require the two issues to be kept separate.

Second, a general property of braided rivers is that greater taxonomic richness and invertebrate density occur in lateral habitats rather than main channels. Karaus (2004), for example, found that > 50 % of overall diversity in the Tagliamento River was contributed by lateral habitats, and we found that > 75 % and > 73 % of lateral habitats contained greater richness and abundance respectively than their associated main

channels. In terms of biodiversity conservation, the value of these lateral habitats cannot be overstated (Arscott et al. 2005).

Finally, due to the spatial and hierarchical structure of diversity in braided rivers conservation managers need to ensure that assessments of biodiversity are made at the appropriate spatial scales. It is not sufficient to categorise the diversity of a river system based on the assessment of a single reach or main channel habitat. The spatial diversity of braided rivers requires lateral and longitudinally stratified sampling to reduce the possibility of spurious conclusions being drawn.

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Chapter 3. Multi-scaled environmental determinism of benthic invertebrate communities in braided rivers: evidence for complex hierarchical controls on local communities

Floodplain pond in the Tukituki River, Hawkes Bay, North Island (top) and spring source in the Landsborough River, South Westland, South Island.

This manuscript is in review for the Canadian Journal of Fisheries and Aquatic Sciences as Gray & Harding. That journals formatting has been retained.

Abstract

Globally many braided river systems have become highly modified, however in their natural state they include a wide range of habitats that support high benthic invertebrate diversity. Here we investigate the determinants of this diversity by assessing the influence of environmental drivers and biogeographic structuring across eleven braided rivers in New Zealand. Within each river, six reaches were sampled and within each reach up to five floodplain habitat types (main channels, side braids, spring sources, spring creeks and ponds). Environmental variables either measured in the field or derived from GIS and hydrological data bases were compared to invertebrate distributions. Communities in all habitat types were influenced by catchment scale hydrology, which partially regulated factors at lesser scales. However, the spatial scale of environmental factors with the greatest influence varied between habitat types. Main channel communities were influenced equally by catchment and habitat scale conditions, whereas spring communities were primarily regulated at the habitat level. There was considerable cross-scale correlation in the effect of environmental factors suggestive of hierarchical controls. We found no independent spatial structuring of invertebrate communities due to collinearity of environmental and biogeographic patterns. Gamma diversity was regulated by the environment across a range of scales. Thus, both hierarchical structure and variation across broad environmental gradients need to be incorporated into conservation planning.

Introduction

Understanding the relative importance of environmental factors operating at differing spatial scales on the diversity and distribution of communities is one of the central themes of ecology (Allen & Starr 1982; Begon *et al.*, 1996; Weins 1989). Regional species pools and factors that influence dispersal provide a template for local diversity and community structure by determining the species available to colonize a particular location (Cornell & Lawton 1992; Ricklefs & Schluter 1993). Environmental conditions and species interactions then determine the local species assemblage. However, the interaction between taxa and environmental conditions may occur across a range of scales or organizational levels, and correlations may exist between variables at different scales. Hence, taxa-environment relations should be viewed as being hierarchical in structure (Frissell 1986; Poff 1997). Assemblages within a single habitat, reach or catchment will be the product of the species pool at a greater spatial scale, as well as dispersal and environmental conditions acting at finer scales. However, hierarchical structure and scale dependence frequently confound our analysis of ecological data, as conclusions made about observations at one spatial scale may in fact represent the effect of factors operating at a different scale (Cushman & McGarigal 2002). This is particularly problematic when there are strong cross-scale correlations between environmental factors. The relationships identified at different spatial scales are not independent and therefore the relative strengths of relationships are difficult to assess. Nevertheless, multi-scale hierarchical approaches are critical to investigations of pattern and process in ecological systems (Lawler & Edwards 2006).

Spatial structuring in community data sets can be interpreted in one of two ways. If the focus of investigation is environmental regulation of communities, spatial autocorrelation constitutes background noise to be controlled (Borcard *et al.* 1992; Lichstein *et al.* 2002; Peres-Neto & Legendre 2010). However, spatial structuring that is independent of the environment can also be used to infer dispersal effects at smaller spatio-temporal scales, and regional or biogeographic patterning at larger scales (Cottenie 2005; Peres-Neto & Legendre 2010). Therein, niche-based models are invoked to explain patterns in diversity and community structure through interactions between fauna and the environment

(MacArthur, 1972; Chase & Leibold 2003; Leibold *et al.* 2004). Alternatively, neutral models (Hubbell, 2001; Leibold *et al.* 2004; Thompson & Townsend 2006) assume ecological equivalence between species and that presence or absence is purely a result of distance (local dispersal and biogeographic pattern).

Many studies of braided rivers have focused on the central channel and have characterised these systems as environments whose communities are regulated primarily by physical disturbance processes (Scrimgeour & Winterbourn 1989; Tockner *et al*. 2006). An expanded view of floodplain systems incorporates lateral habitats such as ponds and springs (Ward *et al*. 1999; Ward *et al*. 2002; Gray & Harding 2009), which despite being part of a single body of water moving down the river valley, have very different physical characteristics. Consequently, we might expect different habitats within a braided river complex to be regulated by different environmental factors operating at different spatial scales and have more or less spatial structuring. Braided rivers are hierarchically structured systems containing heterogeneous spatially nested sub-units replicated across a landscape (Ward *et al.* 2002). Furthermore, braided river floodplains conform to the shifting mosaic steady state model in which habitat turnover is high, but proportions of habitats are constant (Bormann & Likens 1979; Arscott *et al*. 2002; Latterell *et al*. 2006; Whited *et al,* 2007). Thus, rivers in general, and floodplain systems in particular, provide an appropriate arena to further our understanding of the relationships between biological communities, the environment and spatial scale within large natural systems.

The objectives of this study were first to identify environmental and spatial variables that had a significant influence upon invertebrate communities in braided river floodplains at the catchment, reach and habitat scales (Figure 1). Secondly, we quantified the degree of cross-scale correlation between environmental variables in order to isolate confounded and independent effects of environment at any single scale. Thirdly, in order to test the relative effects of individual environmental variables at each scale we removed the effects of spatial autocorrelation and environmental variation acting at greater scales.

Finally, we assessed the relative levels of environmental vs. biogeographic regulation of invertebrate communities within each habitat type.

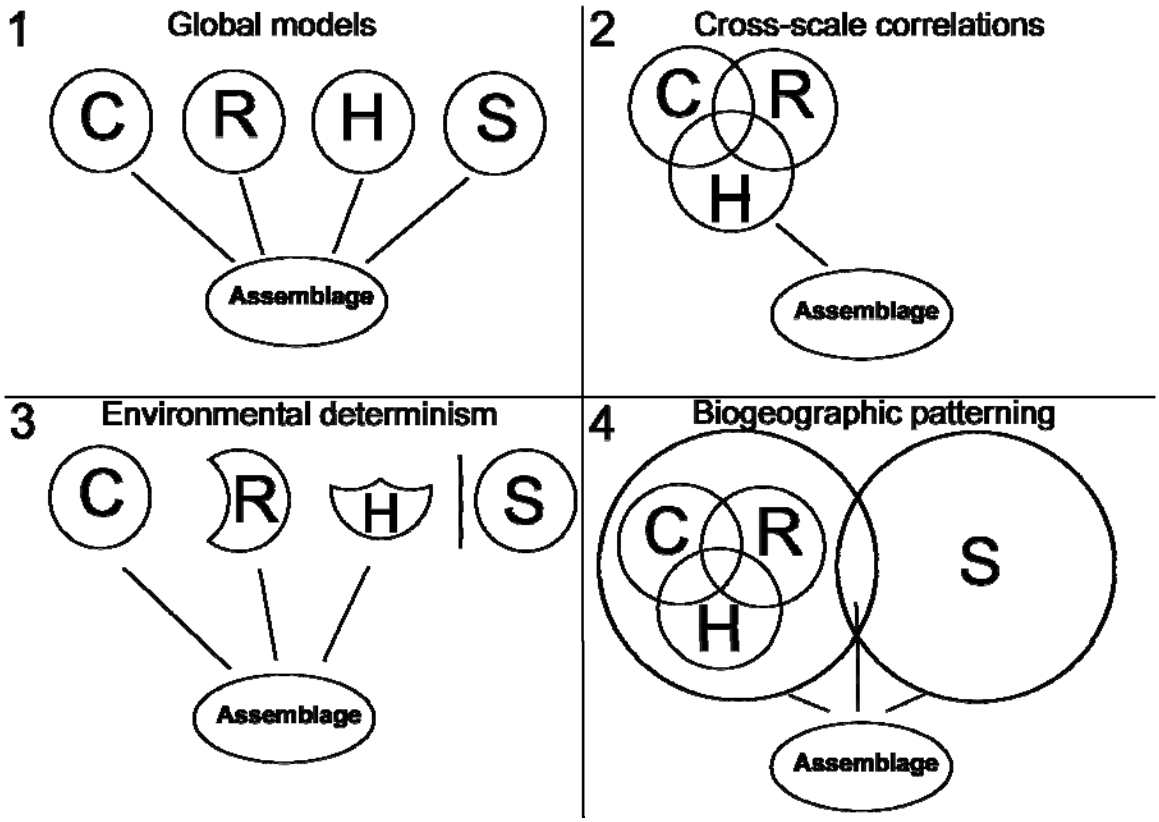

Figure 1. Analytical map illustrating the statistical treatment of variation in invertebrate assemblages. C – catchment scale environmental factors, R – reach scale environment, H – habitat scale environment, S - spatial arrangement of sites. Panels correspond to each of four objectives outlined in the introduction and methods.

Methods

We performed a nested, hierarchical survey of benthic invertebrates in eleven rivers, 3 in the North Island and 8 in the South Island (Fig 2A). Rivers were selected based on the distribution and abundance of braided rivers within New Zealand reported by Wilson (2001). Six reaches ~1 km long, were selected at intervals along each river (Fig 2B), and within each reach up to five habitat types (main channel, side braid, pond, spring source, and spring creek) were sampled (Fig 2B). The uppermost reaches were in the steeper headwaters, above the point where a distinct floodplain first appears on a 1: 50,000 topographical map. In these reaches, the river was generally 3rd–4th order (Strahler

1957). The lowest reach was close to the river mouth, up-stream of estuarine and brackish water zones and tidal influence. Intermediate reaches were distributed evenly between the uppermost and lowermost reaches. Anthropogenic impacts generally increased downstream, although variation was considerable among rivers. A full description of site selection methods is given by Gray & Harding (2009).

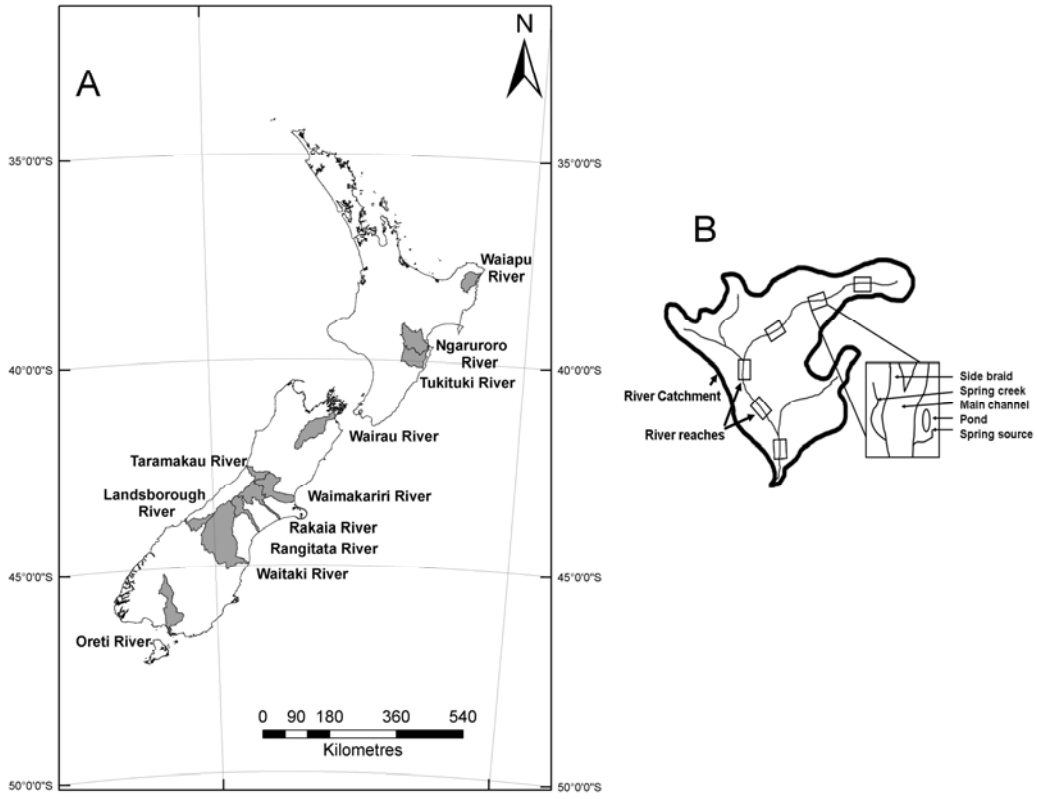

Fig 2A.) Eleven braided river catchments included in the survey, three in the North Island and 8 in the South Island B). Six reaches were sampled within each catchment and five floodplain habitats in each reach.

Three biological samples were collected from each habitat within each reach with a Surber sampler (0.11 m^2, mesh size = 250 μm) at baseflow between December 2006 and April 2007. Quantitative pond samples were taken with the Surber sampler enclosed by mesh within which invertebrates were washed and agitated into the sampler net by hand. Identifications were made to the lowest taxonomic level possible (mostly genus), except for Oligochaeta and Chironomidae, which were identified to sub-family. Full descriptions of invertebrate sampling methods are given by Gray & Harding (2009).

Catchment, reach and habitat variables

Environmental data were collected at three spatial scales; catchment, reach and habitat. Catchment and reach scale variables were derived from a combination of data from the River Environment Classification (REC) (Snelder *et al*. 2005) and the Freshwater Environments of New Zealand (FWENZ) data base (Wild *et al*. 2005) and our own field data. The REC is a stream network database that characterizes waterways using hierarchical categorical descriptors. The FWENZ is an environmental classification of the national river network, based on the REC, but uses continuous variables. We collected further field data to quantify the number, type and successional stages of aquatic floodplain habitats, the type and quantity of coarse woody debris, and the successional stages of terrestrial floodplain elements (recorded every 20 meters the full width of the floodplain). Further hydrological variables were calculated from long-term discharge records maintained by regional councils and the National Institute of Water and Atmospheric Research (NIWA). Stage height loggers were located in the lower reaches of all rivers, and discharge statistics, (e.g. time since a 3 times median flow event) were extrapolated to upstream reaches. Habitat scale data were collected simultaneously during invertebrate sampling using standard techniques (Hauer & Lamberti 1996). Successional stage was assessed using a five part qualitative scale based on the vegetation cover of the terrestrial floodplain surrounding the habitat (Burrows 1977; Reinfelds & Nanson 1993). This procedure resulted in a total of 68 variables: 21 variables at the catchment scale, 25 at the reach scale and 22 at the habitat scale (Table 1). The spatial configuration of habitats and reaches was represented by x and y coordinates derived from the New Zealand map grid (Land Information New Zealand 1995).

Table 1. Environmental variables derived from REC, FWENZ, stage height recordings and field data for the 11 rivers at three spatial scales; catchment, reach and habitat scale.

Scale	Abbreviation	Source	
Catchment	UShardness	FWENZ	average hardness of underlying rocks, 1 = very low to 5 = very high
	USaveslope	FWENZ	average slope in catchment (°)
	USindigfor	FWENZ	areas with indigenous forest (proportion)
	USnative	FWENZ	area with indigenous vegetation (proportion)
	USpeat	FWENZ	area of peat in catchment (proportion)
	USphos	FWENZ	average phosphorus concentration of underlying rocks, 1 = very low to 5 = very high

	UScalcium	FWENZ	average calcium concentration of underlying rocks
	FloodDur	Flow stats	number of events >FRE3 hours in previous 132 days
	FRE3 X	Flow stats	average number of floods per year that exceed three times median flow
	FRE3	Flow stats	days since last FRE3 flood
	FRE6	Flow stats	days since last FRE6 flood
	FRE9	Flow stats	days since last FRE9 flood
	MaxFlood	Flow stats	maximum flow in last 132 days / median flow
	USrain	FWENZ	days/year with rainfall greater than 25 mm
	USglacier	FWENZ	area of glacier in catchment (proportion)
	USlake	FWENZ	area of lake in catchment (proportion)
	Mflow	FWENZ	Mean annual flow (l/s)
	SegFlow	FWENZ	segment mean annual 7 day low flow (cumecs) fourth root transformed, i.e. (low flow + 1) 0.25
	Flow_Var	FWENZ	annual low flow: annual mean flow (ratio)
	Source of flow	REC	Categorical descriptor of source of flow zones
	Climate	REC	Categorical descriptor of climatic zones
Reach	Hrichness	Field survey	richness of habitat/successional types across the floodplain
	Hnum	Field survey	number of habitat types observed across the floodplain
	Hshannon	Field survey	Shannon index of habitat/successional types across the floodplain
	Tsprings	Field survey	total number of springs observed across the floodplain
	Tponds	Field survey	total number of ponds observed across the floodplain
	Lrich	Field survey	floodplain element successional richness
	shannonL	Field survey	Shannon index of floodplain successional types
	Modage	Field survey	floodplain modal successional stage
	MFage	Field survey	floodplain mean age class
	Alt.	survey	altitude
	Lochab	FWENZ	weighted average of proportional cover of local habitat using categories
	LocSed	FWENZ	weighted average of proportional cover of bed sediment using categories
	DFS	REC	distance from source of main channel
	Pdst2s	REC	proportional distance to source
	JanAT	FWENZ	segment January air temperature
	RipSh	FWENZ	segment riparian shade (%)
	Slope	FWENZ	segment slope (degrees)
	ShanFP	Field survey	Shannon index of floodplain successional stage
	LogJam	Field	log jams/ km of transect

		survey	
		Field	
	Logs	survey	logs/km of transect
		Field	
	Wtree.	survey	fallen whole trees / km of transect
		Field	
	Trunks	survey	tree trunks with root wad / km
		Field	
	CWD	survey	coarse woody debris objects / km
	SumT	FWENZ	summer air temperature (ºC)
	TSeas	FWENZ	winter air temperature normalized with respect to SegSumT
		Field	
Habitat	Age	survey	successional stage of surrounding floodplain, 1-5 (5= most mature)
		Field	
	Cond.	survey	conductivity (μS_{25} cm^{-1})
		Field	
	Temp.	survey	temperature (ºC)
		Field	
	pH	survey	pH
		Field	
	DO.	survey	dissolved oxygen (%)
		Field	
	SIJow.	survey	substrate index – (Jowett & Richardson 1990)
		Field	
	MSub.	survey	median substrate size of 30 particles
		Field	
	MxSub.	survey	maximum substrate size of 30 particles
		Field	
	Macro%	survey	% cover of macrophytes
		Field	
	Moss%	survey	% cover of moss
		Field	
	Tcov%	survey	total % cover of aquatic plants including filamentous algae
		Field	
	CPOM	survey	Mean CPOM (g DW) from 3 Surber samples
		Field	
	SuspOrg.	survey	Mean suspended sediment organic component (g) from 5 grab samples AFDW)
		Field	
	SuspSed	survey	Mean suspended sediment (g DW) from 5 grab samples dry weight
		Field	
	SSOrg	survey	Mean stone surface layers organic component (g AFDW) from 3 samples AFDW
		Field	
	Wid	survey	mean width (m)
		Field	
	Depth	survey	Mean depth (m)
	Xdepth	Field	maximum depth (m)

	survey	
	Field	
Wd/dep	survey	Width/depth ratio
	Field	
Vel	survey	Mean velocity
	Field	
pfa	survey	Pfankuch stream stability evaluation (Pfankuch 1975)
	Field	
Turb	survey	turbidity (NTU)

Statistical Analysis

We used multivariate ordination techniques to assess relationships between the spatial arrangement of sites, environmental conditions and invertebrate community composition. The spatial arrangement of sites was represented by map grid coordinates, x, y and all 3rd order polynomials (Borcard *et al*. 1992), and principle coordinates of neighbourhood matrices (PCNM) (Dray *et al*. 2006). However, PCNM were assumed less appropriate for accurately modeling the broad spatial patterns predicted in our data set due to the irregular arrangement of sites and are not presented here (Laliberté *et al*. 2009; Peres-Neto & Legendre 2010). All continuous environmental variables were ln(x + 1) transformed and proportional data were arcsine square-root transformed prior to analysis to meet assumptions of normality and heteroscedasticity. Abundance data from three Surber samples were averaged and Hellinger-transformed to reduce the influence of occasional high densities in some samples, and to control for the effect of rare taxa (Rao 1995; Legendre & Gallagher 2001). The Hellinger distance measure also effectively deals with the "species abundance paradox" associated with Euclidean distance, where the distance between two sites sharing no species can be smaller than that between two sites that share species (Laliberté *et al*. 2009). Initial Detrended Correspondence Analyses (DCA) indicated that a linear ordination method was appropriate (Ter Braak & Smilauer 1998) therefore we opted to use Redundancy Analysis (RDA). During all subsequent analyses we accepted variables and models at $p < 0.10$ to reduce the likelihood of rejecting biologically relevant variables (Legendre & Legendre 1998)

All analyses used adjusted r^2 values (Peres-Neto *et al*. 2006) which provide an unbiased estimate of variance and control for the number of explanatory variables in a model and the number of sites used. Thus, by using the adjusted r^2, it was possible to make a rigorous comparison between different models and components of variation within a partition. The first objective of this study was to identify suites of spatial and environmental variables for each habitat type that significantly influenced invertebrate community composition at each spatial scale (Figure 1; panel 1). Significant explanatory variables were selected using stepwise forward selection (Miller & Farr 1971). Classical forward selection has a tendency to inflate type 1 errors and over estimate the variance explained; these problems were overcome using the procedure of Blanchett *et al*. (2008) as follows. An initial global model, incorporating all predictor variables, was produced. If it was significant after 999 permutation steps, the adjusted r^2 of the global model was used as a stopping criterion for forward selection, along with an alpha level of $p<0.1$. If the addition of any variable into the model exceeded either threshold value, the selection procedure was stopped. If the global model was not significant, forward selection was not performed. Analyses were done using the r package "Packfor 0.0-7" for forward selection and "Vegan 1.15-4" to calculate adjusted r^2 and perform RDA (R Core development team 2009).

For each habitat type we compared the degree of cross-scale correlation between significant environmental variables derived from forward selection at each spatial scale (Figure 1; panel 2). For this we used a hierarchical partitioning of variance to separate confounded and independent effects of environmental factors acting at different spatial scales (Borcard *et al*. 1992; Cushman & McGarigal 2002; Peres-Neto *et al.* 2006). Spatial autocorrelation was left in the model as the spatial structuring of the environment is an important part of the relationship between environmental variables measured at different spatial scales. Analysis was done using the r package "varpart" in "Vegan 1.15-4" (R Core development team 2009). Area proportional Venn diagrams of variance decomposition were produced using Google charts (2009).

We then wished to identify the independent effect on invertebrate community composition of environmental variables at each scale in each habitat (Figure 1; panel 3). It was first necessary to control for spatial autocorrelation [S] (Borcard *et al.* 1992; Lichstein *et al.* 2002). Sites that are closer together often show positive autocorrelation, whereby communities are more similar in composition than sites further apart by virtue of that proximity, and the effect of the environment is obscured. At the catchment scale [C] we used partial-RDA to remove the effect of space before computing the influence of individual variables from the reduced models produced by forward selection. Second, due to cross-scale collinearity of environmental factors identified by hierarchical partitions of variance, it was also important to remove the effect of the environment at greater spatial scales before computing the influence of variables at lesser scales. Therefore, at the reach scale [R] the effects of space and catchment environment were removed, and at the habitat scale [H] the effects of space, catchment and reach were removed. Analyses were performed using partial-RDA in "Vegan 1.15-4" (R Core development team 2009).

Finally, we assessed the degree of biogeographic patterning in braided river communities (Figure 1; panel 4). This was done by partitioning the effects of the combined suite of significant environmental variables [E] (from across the three spatial scales) and space [S] into four components. The components of variation derived from the analysis were [E] environmental variation with any spatial effect, [S] spatial variation with any environmental effect, [E|S] independent environment and [S|E] independent spatial variation. The significance of each component was evaluated using 999 permutations. For the partial-RDA, [E|S] and [S|E], residuals under the reduced model were permuted, but to calculate the significance of [E] and [S] the full model was used (Cottenie 2005). This analysis was done using "RDA" in "Vegan 1.15-4" (R Core development team 2009).

The relative effects of biogeographic patterning and environmental determinism can be inferred from the significance structure of the components of variation from ordinations (see Cottenie 2005). Briefly, assemblages may be determined primarily by

environmental gradients. Dispersal is sufficient to allow all taxa to "sample" a habitat, but does not result in independent spatial patterns because its effect is confounded by environmental gradients. Thus, [S|E] will not be significant, whereas [E|S] will. In contrast, populations may contain regional endemics, which create imperfect species sorting through their absence from suitable habitats (dispersal limitation). Therefore, independent spatial dynamics will occur and both [S|E] and [E|S] will be significant. Finally, if all taxa have an equal response to environmental gradients then only the independent spatial component [S|E] of variation, the effect of biogeographic pattern, will be significant.

Results

We identified 145 taxa from a total of 203 sites. Most individuals (63%) belonged to 5 taxa, of which the leptophlebiid mayfly *Deleatidium* sp. and Orthocladiinae (Chironomidae) comprised (40%) of all individuals. Chironominae, the gastropod *Potamopyrgus antipodarum*, and Elmidae (Coleoptera) complete the list of 5 most common taxa. Of the 145 taxa, 37 were unique to the South Island and 9 were only found in the North Island. Twenty-six taxa were represented by less than six individuals. Invertebrate richness was greatest in the Wairau and Ngaruroro rivers, and least in the Waiapu and Landsborough rivers. Further detail on the diversity and distribution of taxa can be found in Gray and Harding (2009; In Press)

Environmental variables at differing spatial scales

Invertebrate communities varied in their response to specific environmental factors, the scale of regulation and the degree of spatial structuring (objective 1) (Table 2). The global models of space, habitat, reach and catchment scale environment versus invertebrate community for ponds were not significant, and side braid communities were only influenced by space. These habitats are not considered further. Spatial structuring was apparent in main channel and spring source habitats. Although spring creeks and sources were significantly ($p<0.1$) influenced by the environment at all three scales, main channels showed no response to reach-scale variables.

Table 2. Adjusted r^2 and significance values ($p<0.1$ in bold) of global models relating Hellinger transformed invertebrate abundance to space and the environment. Spatial variables were represented by x, y and all 3rd order polynomials. The environment was represented by the variables measured at each spatial scale and listed in table 1. The analyses of space and environment at each spatial scale were performed in isolation such that each result includes effects which are joint with the environment at other scales and/or space.

	Space	Environment		
	xy	Habitat	Reach	Catchment
Main channel	**0.106 (0.005)**	**0.022 (0.005)**	0.00 (0.62)	**0.246 (0.005)**
Side braid	**0.188 (0.005)**	0.0 (0.61)	0.00 (0.51)	0.0 (0.53)
Ponds	0.003 (0.42)	0.0 (0.57)	0.057 (0.25)	0.048 (0.31)
Spring creeks	0.021 (0.31)	**0.307 (0.01)**	**0.162 (0.09)**	**0.151 (0.05)**
Spring sources	**0.11 (0.005)**	**0.274 (0.005)**	**0.111 (0.08)**	**0.207 (0.005)**

Forward selection was applied to each significant global model to produce a reduced model of important environmental variables at each scale and to account for spatial effects. For the main channel, spring creeks and spring sources, variation explained by environment was then partitioned into the joint and independent effects of each spatial scale using a hierarchical decomposition of variance (Objective 2) (Fig. 3). Independent variation is represented by non-overlapping segments of the venn diagram, whilst variation shared between spatial scales is represented by the overlapping portions. Thus, variation joint between two (or three) spatial scales shows the degree of cross-scale correlation. All three habitats showed approximately 30% taxa-environment concordance. Main channel communities responded to a similar degree to both catchment and habitat scale conditions, although catchment scale factors appeared to be more influential overall (Fig. 3). Both spring creek and spring source invertebrate communities were primarily influenced by the habitat scale environment, particularly the spring sources, which showed a strong independent effect of habitat (Fig. 3). Spring creek communities were influenced by reach scale factors, although these were highly collinear with the habitat scale. In contrast, spring source communities were less affected by reach scale factors and reach environment had negligible independent effects. Catchment effects were of

similar magnitude for both spring habitats, but they were entirely independent of reach effects in spring creeks, whereas there was considerable overlap between scales for spring sources.

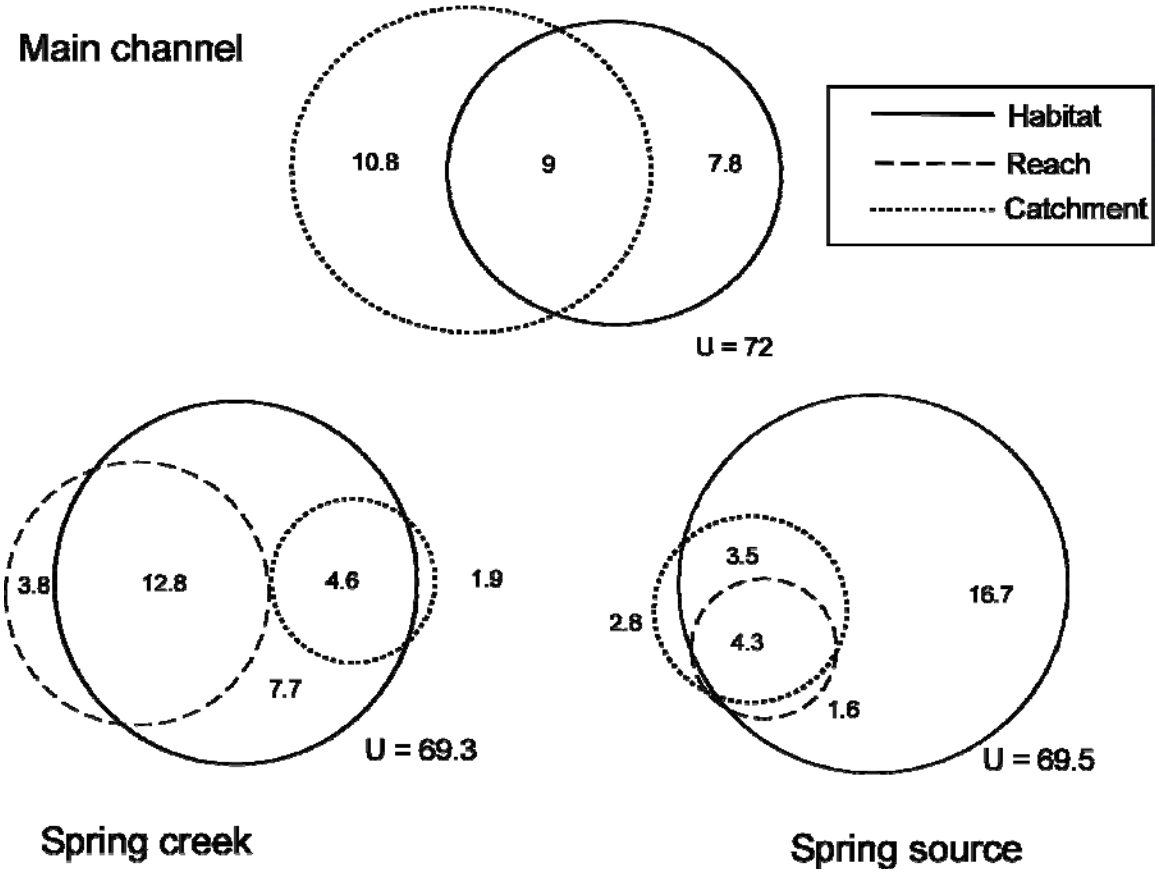

Fig 3. Hierarchical decomposition of variance in invertebrate communities related to the environment measured at three spatial scales in three habitat types on braided river floodplains. The percentage of total variance explained by the different individual components is shown. The area of each circle and overlap is proportional to its explanatory power. The unexplained percentage of variation (U) is shown below each plot. Spatial variation is included in the models.

Environmental drivers of community composition

The invertebrate communities of main channel habitats showed significant spatial structuring. Once spatial autocorrelation had been removed, invertebrate communities were found to be regulated strongly by hydrological conditions; both in terms of recent and long term flow regimes (objective 3) (Fig 4 C|S). Sites with stable flows, such as the impounded lower Waitaki, were located to the right of RDA Axis 1, whereas locations that experienced more frequent flood events were positioned to the left of Axis 1.

Proportion of the up-stream catchment in native forest was also influential and negatively correlated with base-flow of the site. At the habitat scale in the absence of both spatial autocorrelation and influence of catchment scale factors (i.e. the independent effect of habitat scale), communities were regulated by quantities of CPOM and substrate size (Fig 4 H|C, S). The effect of stream bed disturbance was also important.

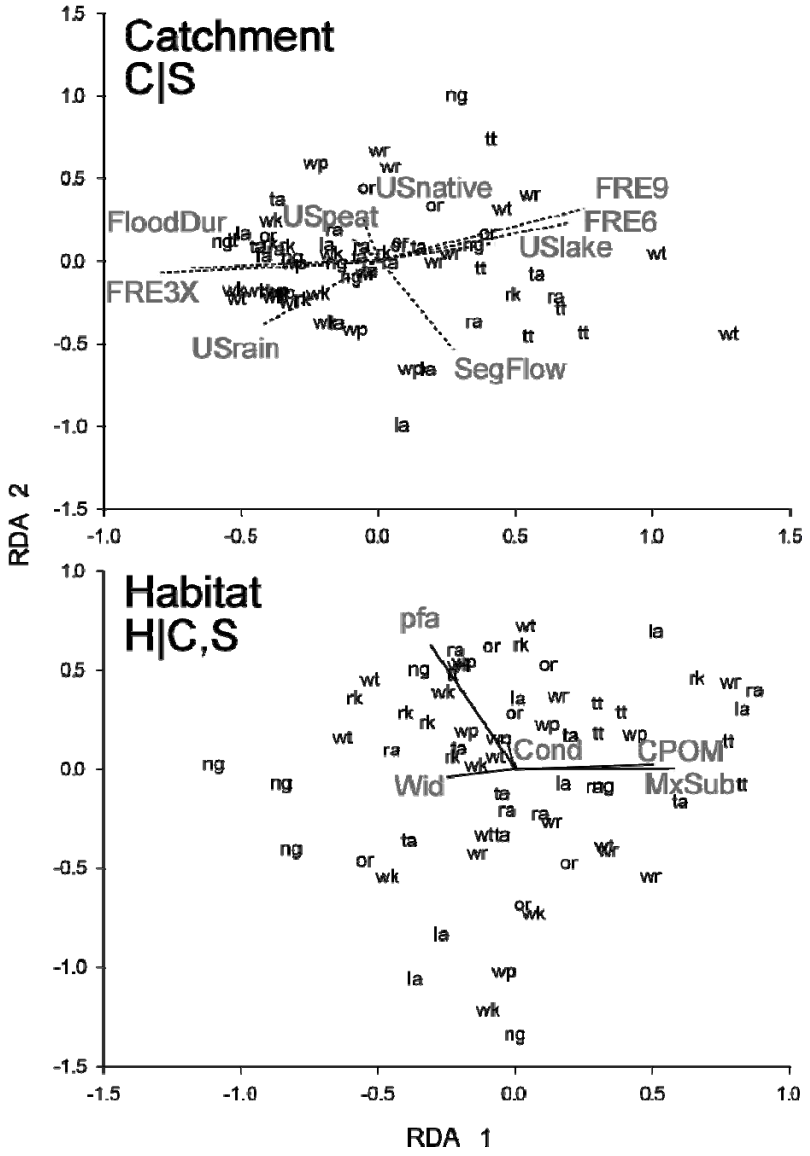

Figure 4. RDA plots of main channel invertebrate community composition (Hellinger transformed) in relation to environmental variables measured at the catchment (C|S) and habitat (H|C,S) scales. At the catchment scale spatial autocorrelation has been removed and at the habitat scale the effects of space and catchment environment have been removed. Codes for environmental variables are in Table 1. Rivers codes are la, Landsborough; wp, Waiapu; rk, Rakaia; ra, Rangitata; wk, Waimakariri; tt, Tukituki; wt, Waitaki; or, Oreti; ta, Taramakau; wr, Wairau; ng, Ngaruroro.

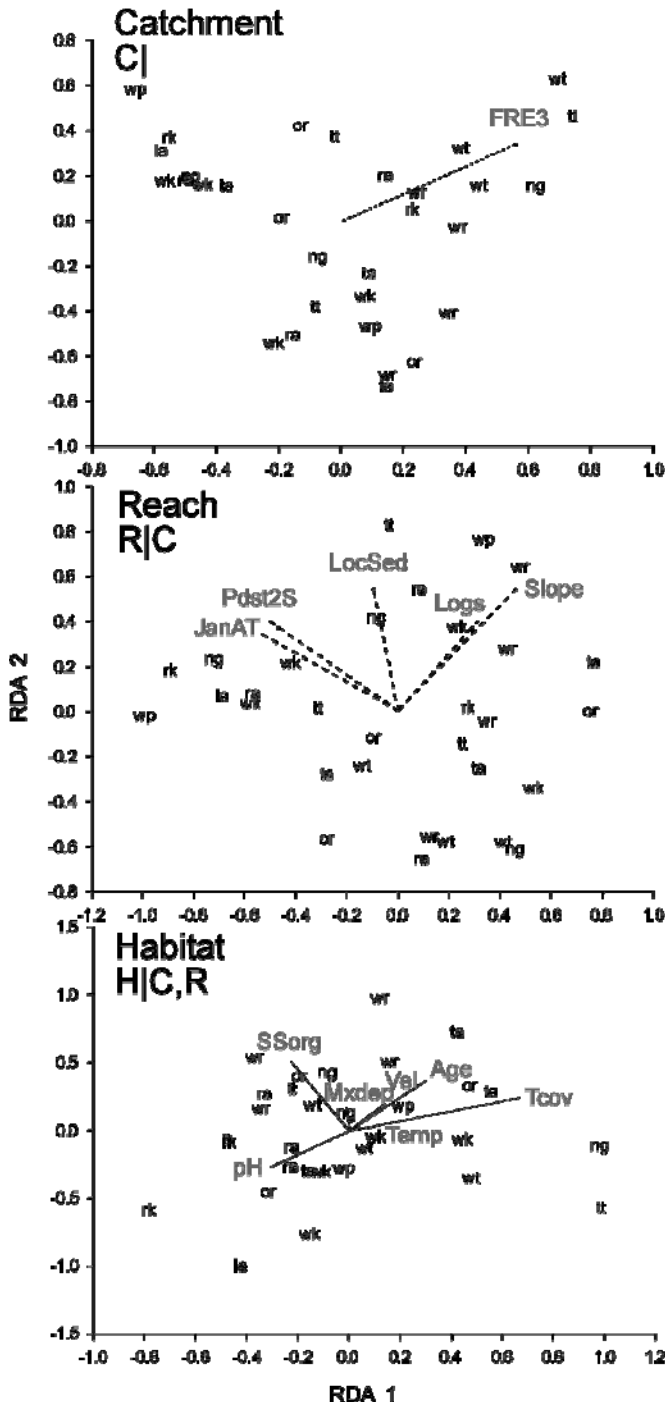

Figure 5. RDA plot of spring creek invertebrate community composition (Hellinger transformed) in relation to environmental variables measured at the catchment (C|), reach (R|C) and habitat (H|C,R) scales. At the reach scale the effect of catchment scale environment has been removed and at the habitat scale the effects of catchment and reach environment have been removed. Codes for environmental variables are in Table 1. Rivers codes are la, Landsborough; wp, Waiapu; rk, Rakaia; ra, Rangitata; wk, Waimakariri; tt, Tukituki; wt, Waitaki; or, Oreti; ta, Taramakau; wr, Wairau; ng, Ngaruroro.

Invertebrate communities in spring creeks showed no spatial autocorrelation. The only important catchment scale variable was the time since the last 3X median flow flood (FRE3) in the main river (Fig. 5 C|). After the removal of the effect of FRE3, communities were found to be influenced by reach scale factors, specifically January air temperature and proportional distance to the spring source (Fig. 5 R|C). Sediment size, woody debris and slope were also important. In the absence of catchment and reach scale factors spring creek communities were primarily influenced by successional processes: spring age, total cover of aquatic plants and the organic content of stone surface layers (Fig. 5 H|C, R).

By contrast spring sources showed significant spatial structuring. After removal of spatial patterns, communities were also regulated primarily by the hydrology of the main river at the catchment scale (Fig. 6 C|S). Influential environmental factors were number of days with >25 mm of rain per year (USrain), the number of FRE3 flood events in the last 132 days (FRE3X) and mean flow (Mflow).

At the reach scale, communities were regulated by the average age of the floodplain (MFage) and slope, although these effects were entirely collinear with variables measured at the habitat scale (Fig. 6 R|C, S). Influential habitat variables were age and total cover of aquatic plants (Tcov), substrate, velocity and stream width (Fig. 6 H|C, R, S).

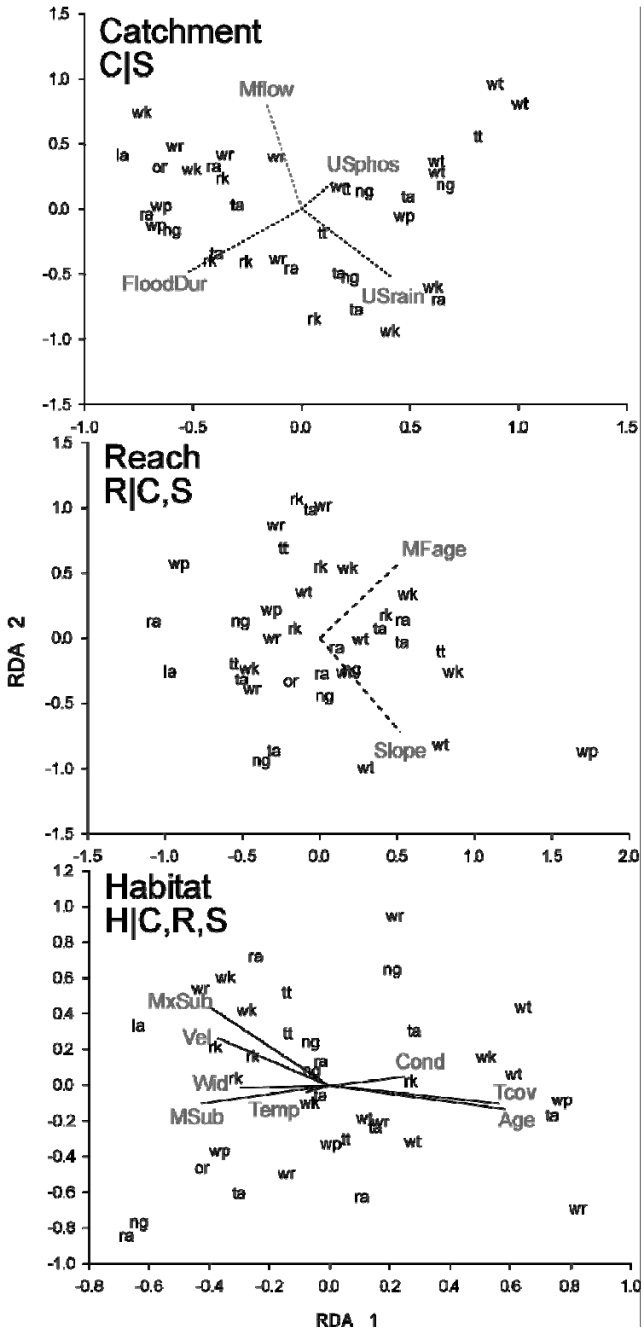

Figure 6. RDA plot of spring source invertebrate community composition (Hellinger transformed) in relation to environmental variables measured at the catchment (C|S), reach (R|C, S) and habitat (H|C,R,S) scales. At the catchment scale spatial autocorrelation has been removed, at the reach scale the effect of space and catchment environment has been removed and at the habitat scale the effects of space, catchment and reach have been removed. Codes for environmental variables are in Table 1. Rivers codes are la, Landsborough; wp, Waiapu; rk, Rakaia; ra, Rangitata; wk, Waimakariri; tt, Tukituki; wt, Waitaki; or, Oreti; ta, Taramakau; wr, Wairau; ng, Ngaruroro.

Biogeographic structuring of invertebrate communities

The joint and independent effects of spatial and environmental (at all scales) variables were tested for each habitat type (objective 4) (Table 3). All habitats showed a significant response to the environment, with [E], and without [E|S], a spatial component (this could not be explicitly tested for spring creeks as no spatial variables were found to be significant). However, no habitats showed independent spatial structuring [S|E] and only main channels showed significant spatial structuring with an environmental component [S]. This indicated that communities in individual habitat types are entirely regulated by environmental factors, which where collinear with biogeographic gradients.

Table 3. The significance of spatial and environmental components of variation in invertebrate community composition calculated using 999 Monte Carlo permutations. Components are S|E pure space, S space with an environmental component, E environment with a spatial component and E pure environment. *na - analysis was not performed as the global model was non-significant and no spatial variables predicted invertebrate communities.

	S|E	S	E	E|S
Main channels	0.67	**0.005**	**0.005**	**0.005**
Spring creeks	na*	na	**0.005**	na
Spring sources	0.24	0.35	**0.005**	**0.005**

Discussion

An environmental template for catchments, reaches and floodplain habitats

At the catchment scale the major drivers of benthic invertebrate communities were descriptors of hydrology, which showed considerable collinearity with environmental determinants at lesser spatial scales. This suggests a strong relationship between hydrology, reach and habitat heterogeneity within braided rivers. Extreme rainfall and flooding reset the floodplain habitat mosaic. The result of flooding is that successional diversity of habitats is reduced, and invertebrate community composition and richness are altered more strongly than in a less regularly disturbed system (Ward *et al*. 2002; van der Nat *et al.* 2003). Multiple studies have shown the applicability of the shifting mosaic steady state model to braided rivers where habitat turnover is high, but proportions of successional habitats are constant (Bormann & Likens 1979; Arscott *et al*., 2002; Latterell *et al*. 2006; Whited 2007). However, glacier-fed and rainfall-fed braided rivers

are subjected to very different sediment loads and flow regimes, and therefore might be expected to vary in overall proportions of habitats and therefore invertebrate diversity and composition. Consequently, we might predict that the invertebrate assemblages of different reaches within any one river would be more similar than between the same reach in different rivers; the reaches of a river would cluster together on an ordination plot. However, closer scrutiny of partial-RDAs (Figs 4, 5 & 6) invites a more subtle conclusion. Different reaches within several rivers, most notably the Ngarururoro, Wairau and Taramakau, exhibited considerable variation in benthic communities (sites are separated on the ordination plot). Therefore, the effects of catchment scale hydrology may be altered by reach scale factors (such as floodplain constriction, vegetation or land use), or habitat scale factors (such as substrate and successional stage) thereby partially de-coupling reach scale morphology from larger scale factors (Stanford & Ward 1993; Gurnell *et al*., 2002; Arscott *et al*., 2003). This scenario suggests there are likely to be complex hierarchical controls on the occurrence and permanence of braided river habitats, and hence their benthic invertebrate communities (Allen & Starr 1982; Arscott *et al*. 2003; Thorp *et al*., 2006).

Extreme flood disturbances are a defining physical characteristic of braided rivers (Arscott *et al*. 2002; Tockner *et al*. 2003; Gray & Harding 2007). However, different habitat types within the floodplain varied in their response to hydrological disturbance. Main channel invertebrate communities in this study appeared to be strongly influenced by long term and antecedent hydrology triggering a shift in community assemblage with increasing flood disturbance. This result has been observed previously in braided rivers such as the Rakaia and Tukituki in New Zealand and Tagliamento in Italy (Sagar 1986; Fowler & Death 2000; Arscott *et al*. 2003). In the main channel of the Tagliamento River, faunal density and richness were greatest during summer low flows and lowest following autumnal floods (Arscott *et al*. 2003) but New Zealand's maritime climate results in seasonally unpredictable flooding relative to more continental climates in Europe (Winterbourn 1997). Nevertheless, geographic and seasonal variation in the timing of floods, and corresponding variation in the composition of invertebrate communities, does occur and is apparent in the findings of this study. In the alpine-

sourced rivers of the South Island, the majority of flooding occurs in the austral spring as a result of snow melt. But in the foothill-sourced rivers of the North Island and the southernmost river(s) in the South Island (e.g. Oreti River), floods occur mainly in winter and are associated with rainfall from southerly storms generated in the sub-Antarctic (Duncan & Woods 2004). The patterns of antecedent flooding (i.e. time since *x* magnitude flood event) in this study, were strongly influenced by this geographic and seasonal variation in the flow regime of particular rivers; alpine versus foot-hill catchments. For example, invertebrate communities in main channels were highly correlated with time since the last flood (FRE6 and 9) which in summer, was greater in foothill-sourced rivers than alpine-sourced rivers. Braided river main channel and side braid invertebrate communities include species that persist despite regular flood disturbance and a combination of behavioural and life history traits, such as drifting, multi-voltinism and seasonal asynchronicity, confer resilience to these communities despite the unpredictable timing of floods (Scrimgeour & Winterbourn 1989; Matthaei & Townsend 2000). However, a discharge that substantially moves substrate will reduce both richness and abundance of taxa (Scrimgeour *et al.* 1988; Matthaei & Townsend 2000) and complete recovery from a catastrophic flood (e.g. 33 times mean discharge) in the Ashley River took 130 days (Scrimgeour *et al*. 1988).

In contrast to main channels, benthic communities of lateral floodplain habitats, spring creeks and spring sources were more influenced by habitat scale factors associated with variations in successional age, aquatic plant beds, organic matter availability; indirect effects of flooding or its absence. High successional diversity of floodplain and aquatic habitats has been observed along the Tagliamento River, (Arscott *et al*. 2002; van der Nat *et al*. 2003) and the upper Waimakariri River, New Zealand (Reinfelds & Nanson 1993) as a consequence of flood events across the floodplain. Furthermore, braided rivers, and particularly their lateral habitats, are highly groundwater-dependent ecosystems (Boulton & Hancock 2006) with habitats differentiated by their degree of vertical hydrological connectivity to the main channel and underlying aquifer (Tockner *et al*. 1999; Brunke 2002). Whilst horizontal connectivity in the form of over-bank flooding is primarily a successional re-setting process, the subsequent successional trajectory of a habitat will be

dictated by vertical exchange and local physical and biological context, such as substrate, altitude and source of colonists. The groundwater, which supplies the lateral habitats of any given reach of a braided river is derived predominantly from the river itself in the form of multi-scaled groundwater – surface water exchange (Brunke & Gonser 1997; Woessner 2000; Pepin & Hauer 2002; Brunke *et al*. 2003). Therefore, despite the apparent physical isolation of lateral habitats they remain a part of the integrated whole. The results of the present study indicate that although hydrological disturbance is the major determinant of invertebrate communities, its influence is manifested in complex ways between habitats and at different scales.

Biogeographic structuring of invertebrate communities

The significance structure of spatial and environmental components of variance within individual habitat types suggests an over-riding influence of the environment on invertebrate communities. This conclusion is in accordance with other studies of braided river invertebrate communities (Sagar, 1986; Arscott, *et al*. 2005), but is not consistent with the view that high levels of regional endemism are found in New Zealand stream invertebrate communities (Boothroyd, 2000). The presence of regional endemics should create spatial structuring as they are effectively taxa with limited dispersal, and therefore absent from environmentally suitable habitats outside their range (Ng *et al,* 2009).

In an analogous study of the spatial and environmental determinants of invertebrate communities in headwater streams Mykra *et al*, (2007) found a positive relationship between the explanatory power of an environmental variable and its range of variation. Therefore, across scales of observation, or ecological systems, such as tropical forests (Hubbell 2001), where environmental gradients are slight, spatial dynamics are likely to be more important. However, in a disturbance driven system with extreme environmental gradients where the majority of individuals are cosmopolitan and not dispersal limited, environmental determinism might be expected to be more influential.

From a meta analysis of structure in 158 temperate communities Cottenie (2005) suggested that those with a spatial scale >1000 km were more likely to be structured by

spatial processes. The maximum distance between sites in our study was 1300 km and although the North and South islands are separated by ≈25 km of sea, no significant effect of spatial structuring was apparent. We suggest that any biogeographic influences on communities are subsumed within the shared environment-spatial component of variation. Given the broad latitudinal reach of the New Zealand landmass and strong climatic gradients this result is not surprising.

Two caveats must be mentioned here; firstly, the low levels of spatial structuring may have been exacerbated by the level of taxonomic resolution used. Greater resolution particularly among chironomids, the leptophlebiid *Deleatidium*, crustaceans, especially subterranean amphipods and hydrobiid snails may have revealed stronger spatial patterns. Secondly, many of the regionally endemic taxa were rare, and did not contribute significantly to the "community" as assessed by ordinations based on quantitative data.

In conclusion we found that braided river invertebrate communities were strongly regulated by environment factors at a range of spatial scales, and that considerable cross-scale correlation indicated complex hierarchical controls. Main channel invertebrates were primarily regulated by catchment scale hydrology, whereas lateral floodplain habitat communities responded to successional processes. Floodplain communities responded to environmental gradients, which appeared to be collinear with biogeographic patterns in the sampled rivers. Our results have important implications for the management of extant braided river systems. Whilst braided rivers have traditionally been regarded as disturbance-dominated, species-depauperate habitats, it is now apparent that overall they incorporate high invertebrate diversity. Programs concerned with the conservation of braided river systems should incorporate this hierarchical environmental determinism within catchments and acknowledge the value of lateral floodplain habitats. Furthermore, as communities varied with, and biogeographic patterns correlated with, the broad-scale environment, protected catchments should be replicated along these gradients.

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Prologue to chapters 4 & 5

Artist: Michelle Greenwood

In the latter part of this thesis I report on an investigation into the role of groundwater-surface water exchange, specifically spring stream ecotones, in the structure and function of floodplain systems. Little is known about the aquatic invertebrate food webs or basal resources that exist in spring streams, and especially the aquifers that supply them. Food webs in surface-flowing streams are most likely founded upon in-stream algal production or terrestrial inputs from surrounding grasslands and forest. Because of a complete absence of light there is no photosynthetic fixation of carbon within an aquifer, and the basis of life is presumed to be organic matter, either dissolved within down-welling surface water, or derived from buried materials (Fenwick 1987; Fenwick et al. 2004). The most common causes of organic matter burial in braided river floodplains are associated with migration of the active river channel (Reinfelds & Nanson 1993), and via tributary sediment pulses (Goff & McFadgen 2002; Korup 2004). Thus, the role of terrestrial vegetation in providing the basal resource within aquifer and spring streams is hypothesised to be two-fold. Buried vegetation may interact with groundwater flow paths to sustain carbon limited phreatic (sub-surface) populations, and the deposition of organic matter into upwelling spring streams might also contribute to surface stream food-web dynamics (Scarsbrook & Townsend 1994; Young et al. 1994).

Recent research has highlighted the role of cross-ecotone subsidies in structuring invertebrate communities (Nakano et al. 1999; Nakano & Murakami 2001) and led to my interest in possible interactions between aquifer and spring stream organisms. Gray

(2005) found numerous ground water invertebrates in springs and spring creeks and a number of surface water invertebrates use groundwater habitats (Burrell 2001). Therefore, the potential is there for food web structure to be affected and subsidised in both surface and sub-surface environments.

To investigate these questions I used stable isotope ratios: nitrogen (^{15}N:^{14}N) and especially carbon (^{13}C:^{12}C). Nitrogen isotope ratios fractionate more-or-less predictably at each trophic level, and can be used to infer the level of feeding activity of individuals or taxa within a community. Carbon conversely, fractionates little as a result of trophic transfer and can therefore be used to infer the basal resource of a system (Fry 2006). However, inferences based on carbon require that potential sources have distinct isotopic signatures, a requirement that depends on the provenance of that carbon (Winterbourn 2000; Fry 2006). The pioneering studies in the use of stable isotopic ratios of carbon to investigate trophic relationships in streams were performed in New Zealand in the early 1980s (Rounick et al. 1982; Rounick & James 1984; Winterbourn et al. 1984). These studies included the analysis of invertebrates and plants from numerous streams, both shaded and open, and included several springs. The most notable features of the spring streams were the highly depleted carbon values of invertebrates relative to those from run-off based streams. This depletion in ^{13}C appeared to be linked to the subterranean residence of carbon and might therefore provide a basis for obtaining insights into floodplain carbon cycles.

In order to assess the potential value of the stable isotope approach I carried out a pilot study involving a single spring in the floodplain of the Hawdon River, Canterbury. I collected food-web components from the spring source and at 300 m and 1000 m downstream, stored the material on ice and returned to the laboratory. Invertebrates were sorted, identified and eviscerated, and contaminant material was removed from algal and other plant samples. All material was ground in a mortar and pestle before being sent to the Waikato Stable Isotope Unit for analysis.

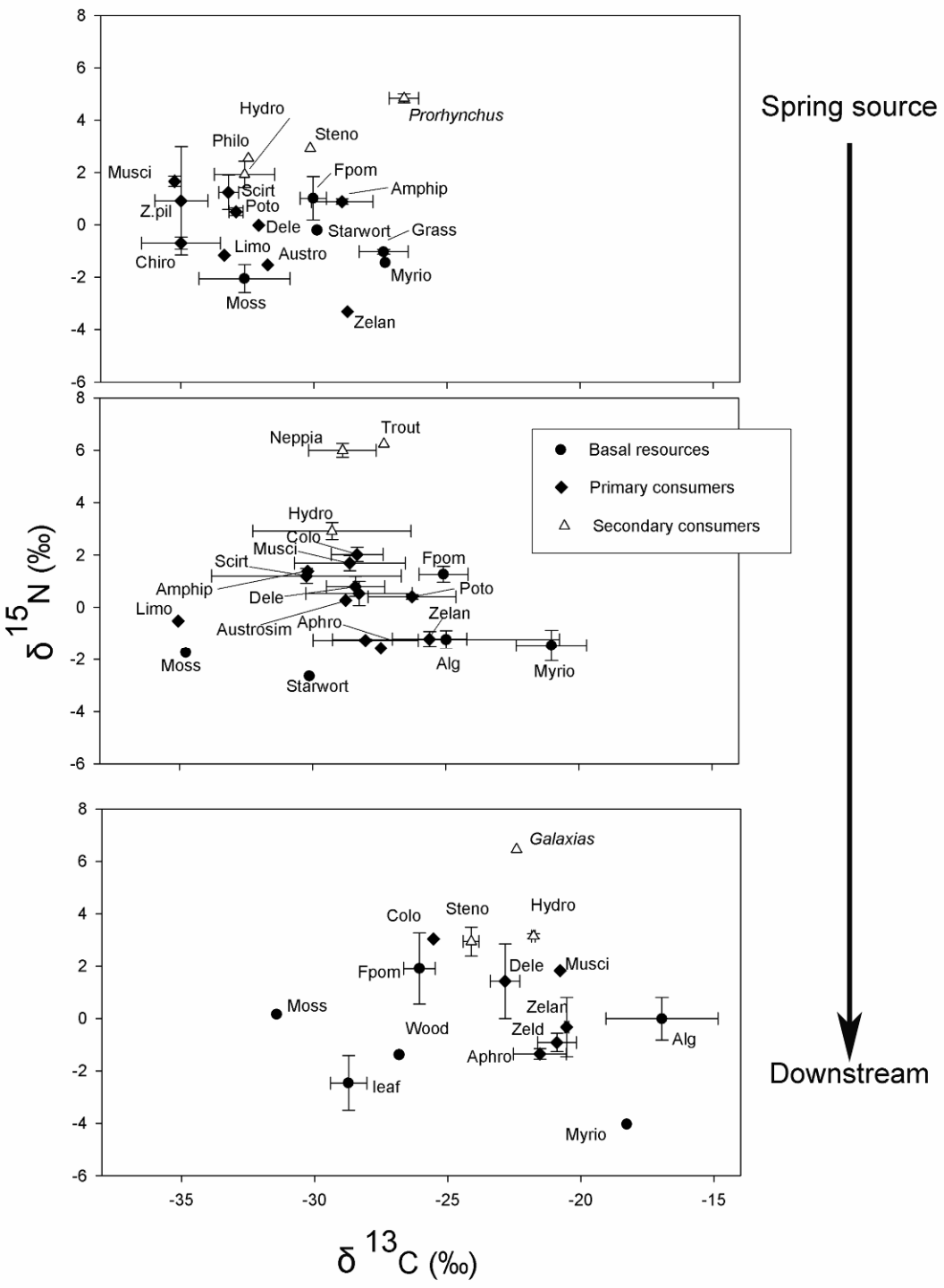

Figure 1. Carbon and nitrogen stable isotope plots of food-web components at three sites along a spring stream in the Hawdon valley. Error bars indicate 1 standard deviation. Invertebrate abbreviations are as follows; Hydro – Hydrobiosidae, Philo - *Philoreithrus agilis*, Steno – *Stenoperla maclellani*, Scirt – Scirtidae, Dele -*Deleatidium* sp., Colo - *Coloburiscus humeralis*, Zelan – *Zelandoperla* sp., Z. pil – *Zelandobius pilosus*, Zeld – *Zelandobius* sp., Austro – *Austroperla cyrene*, Amphip – *Paraleptamphopus* sp., Musci – Muscidae, Aphro – Aphrophila, Limo – *Limonia* sp., Poto – *Potamopyrgus antipodarum*, Austrosim – Austrosimuliidae, Chiro – (non predatory) Chironomid, Alg – filamentous algae, Myrio – *Myriophyllum* sp, Starwort – *Callitriche* sp, Fpom – Fine particulate organic matter (<0.5mm).

A summary of the results obtained is given in Figure 1. Two major features in the carbon v nitrogen biplot indicated that the method had great promise. Firstly, there was a distinct downstream shift in the $\delta^{13}C$ signature. At the spring source several invertebrate taxa showed unusually depleted carbon values (<-30‰) which fell beyond the range expected for carbon of autochthonous or allochthonous origin. However, at the lower sites all invertebrate carbon values were in accord with expected values (>-29‰). Secondly, two groundwater taxa were collected at the spring source, the amphipod *Paraleptamphopus* sp. a collector-browser, and the predatory flatworm *Prorhynchus* sp. Both taxa had carbon values that differed from the other invertebrates examined in being several ‰ more enriched. Provisionally, this suggested that the groundwater taxa, despite co-habitation with the stream taxa, were using a different carbon source, at least in part.

The pilot study therefore confirmed the occurrence of distinct carbon isotope values associated with upwelling groundwater, although not necessarily with groundwater taxa. Furthermore, the results indicated there must be a mechanism, either physical or biological, which caused carbon values within invertebrate food-webs to shift by ~10 ‰ along 1000 m of stream. Thus, new questions arose:

1. What is the origin of the deplete carbon incorporated into spring stream food-webs?
2. Is the longitudinal pattern found in the pilot study a general feature of spring streams in braided river floodplains?
3. Can I observe evidence for cross ecotone organism based transfers of carbon between groundwater and stream?

These questions are addressed in the following two chapters of this thesis.

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Chapter 4. Carbon cycling in braided river floodplain ecosystems: rapid out-gassing of carbon dioxide transmits $\delta^{13}C$ gradient through the stream food-web.

The source of the Taramakau valley spring before (above) and after (below) the prevention of out-gassing using continuous polythene sheeting.

Abstract

Un-impacted braided river floodplains typically possess high vertical hydrological connectivity. This high surface-subsurface exchange is thought to be highly important in the overall function and structure of these complex 3-dimensional systems. Spring -fed streams on the floodplain are hotspots of benthic invertebrate diversity and productivity. $\delta^{13}C$ values of both dissolved inorganic carbon (DIC) and food-web components from springs are unusually deplete and yet this natural abundance tracer has not been used to study the transport and retention of groundwater carbon in floodplain systems. I sampled DIC, and components of aquatic and riparian food-webs from five sites along five floodplain spring systems. Partial pressures of CO_2 in upwelling water ranged from 2-7 times atmospheric pressure, but rapidly approached equilibrium downstream commensurate with an enrichment in $\delta^{13}C$ of DIC. These results indicated both out-gassing and photosynthetic drawdown by aquatic plants might be responsible for the flux of CO_2. A fully factorial whole stream manipulation was then conducted in five springs by preventing out-gassing and photosynthesis. The results of this manipulation indicated out-gassing to be the primary driver of enrichment in $\delta^{13}C$ of DIC. The gradient in $\delta^{13}C$ was transmitted through three trophic levels of the spring food-web, but not observed in riparian predators. These findings indicate a high dependency on groundwater carbon in spring streams and the strong hydrologically mediated linkages which connect terrestrial, subterranean and aquatic components of the floodplain.

Introduction

Many natural rivers have extensive flood-plains that have a diverse array of habitats. In these systems, floodplain habitats are in a state of continual successional change (Arscott et al. 2000; van der Nat et al. 2003). These floodplains are hydrologically connected to the river and wider catchment (Brunke & Gonser 1997; Ward et al. 1999; Woessner 2000) and spatially and temporally variable in groundwater surface-water exchanges (Stanford & Ward 1993; Brunke & Gonser 1997; Poole 2002). Thus, braided river floodplains are typified by a complex 3-dimensional mosaic of heterogeneous habitats along the river and across the floodplain. Feedback loops and interdependence between this diverse array of habitats, and the wider catchment, have been inferred (Hynes 1975; Stanford 1998; Wiens 2002) and more recently demonstrated, particularly links between hydrology and ecology, and between organisms across habitat boundaries (Paetzold et al. 2005; Malard et al. 2006; Tockner et al. 2006). Furthermore, over the last century, biogeochemical studies have been applied to riverine systems uniting aquatic and terrestrial ecology. As a result, Hynes (1975) original assertion that the "stream is ruled by its valley" has received renewed attention (Fisher et al. 2004).

Early biogeochemical studies of streams focused on small, forested headwater systems and consequently on the sources and dynamics of organic carbon in heterotrophic food-webs (Fisher & Likens 1973). Dissolved inorganic carbon (DIC) forms the base of the autotrophic food-web, an important source of energy for streams with adequate sunlight to drive photosynthesis (Raven et al. 1985; Sand-Jensen & Frost-Christensen 1998). From a wider ecosystem perspective the distinction between organic and inorganic carbon may in fact be misleading as the two are interchangeable through the metabolic processes of respiration and photosynthesis (Shibata et al. 2001). However, whilst hydrologists and geochemists are aware of the catchment and in-stream biological controls acting upon DIC (Clark & Fritz 1997; Jones & Mulholland 1998; Telmer & Veizer 1999; Doctor et al. 2008), there is a paucity of studies linking catchment driven DIC to in-stream ecological patterns. That DIC may be the primary source of carbon to a stream food-web, and that the sources of that DIC are varied and complex have been inferred (Finlay 2003; Hawke & Polaschek 2005), but few studies have identified and

traced the signature of $\delta^{13}C$ DIC through a stream food-web (Rounick & James 1984; Finlay 2004; Jepsen & Winemiller 2007).

Inorganic carbon, predominantly in the form of CO_2, is fixed by photosynthesis, in both terrestrial and aquatic environments. The resultant organic carbon is then available to consumers within the stream food-web, either *in situ* (autochthonous), or via inputs from the terrestrial environment (allochthonous). In streams the amount of inorganic carbon available to primary producers is dictated by the balance between atmospheric diffusion, in-stream metabolism, and when present, groundwater inputs (Allan & Castillo 2007). Atmospheric diffusion results in a shift in the CO_2 concentration of water towards that of the atmosphere (387 ppmV), whereas in-stream metabolism will either increase or decrease CO_2 concentration depending on the balance between photosynthesis (-ve) and respiration (+ve) (Fisher & Likens 1973). Finally, groundwater is generally supersaturated with CO_2 due to soil respiration within the catchment (Dawson et al. 1995; Jones & Mulholland 1998). For example, groundwater in the Sleepers River watershed, Vermont, U.S.A. showed a positive excess partial pressure of carbon dioxide ($ePCO_2$) 4-74 times that of the atmosphere (Doctor et al. 2008). The relative effects of the homogenizing influence of the atmosphere, positive effect of groundwater inputs, and variable effects of in-stream processes varies with stream geomorphology, discharge and productivity, as well catchment geology and terrestrial ecosystem productivity and structure (Finlay 2003).

Stable isotope ratios of carbon are a valuable tool for inferring sources and cycling of carbon within ecosystems because the potential sources of carbon (atmospheric, biogenic and geologic) can have broadly distinct signatures. Stable isotope values are conventionally expressed using Delta (δ) notation, in which the ratio $^{13}C:^{12}C$ is given relative to the international standard:

$$\delta^{13}C\ (‰) = (R_{sample} / R_{standard} - 1) \times 10^3$$

where: $R = {}^{13}C:{}^{12}C$.

The evolution of $\delta^{13}C$ DIC begins with dissolution of atmospheric CO_2 (-8‰) by meteoric water (i.e., rainfall). DIC is generally depleted by the further dissolution of CO_2 within soils whose $\delta^{13}C$ value is dependent on the photosynthetic pathway of the predominant surface vegetation. The C_3 pathway operates in about 85% of plant species and predominates in most terrestrial ecosystems (Clark & Fritz 1997). Most C_3 plants have $\delta^{13}C$ values that range between -24‰ and -30‰ with an average value of -27‰ (Clark & Fritz 1997). Photosynthetically fixed carbon in the form of vegetative matter accumulates within soils where aerobic bacteria convert the majority of carbon back into CO_2, resulting in soil CO_2 concentrations 10-100 times greater than in the atmosphere. Microbial and plant root respired CO_2 has the same $\delta^{13}C$ value as the source vegetation, although out-gassing from soils may result in isotopic enrichment in excess of 4‰ (Cerling et al. 1991; Aravena et al. 1992, but see Davidson 1995). Therefore, the $\delta^{13}C$ of aerobic soils and soil water DIC in C_3 dominated (New Zealand) landscapes can be expected to be approximately -23‰. A further addition to soil and groundwater DIC is HCO_3^- derived from weathering of bedrock. Carbonate dissolution by carbonic acid produces a $\delta^{13}C$ DIC value intermediate between that of soil CO_2 and the carbonate source, whereas HCO_3^- derived from silicate weathering will be 7 to 10‰ greater (more enriched) than the $\delta^{13}C$ value of CO_2 (Kendall et al. 1992; Pawellek & Veizer 1994). The $\delta^{13}C$ value of most carbonates is approximately 0‰ (Craig 1953; Taylor & Fox 1996). Depleted $\delta^{13}C$ DIC values of groundwater relative to surface water have been reported in numerous studies (e.g. Doctor et al. 2008), and have been collated by Finlay (2003).

Upon exposure to the atmosphere at the groundwater–surface water ecotone both DIC concentration and the $\delta^{13}C$ value of DIC may change rapidly through fluxes of CO_2. Isotopic enrichment of DIC in stream water can occur through invasion of atmospheric CO_2 ($\delta^{13}C$ -8‰) (Taylor & Fox 1996). Furthermore, because groundwater is supersaturated with CO_2, there may be a loss of CO_2 to the atmosphere by out-gassing. This results in isotopic enrichment of the remaining DIC as HCO_3^- is converted to CO_2 to maintain the ionic balance of carbonate species (Hendy 1971; Doctor et al. 2008). Finally, in-stream metabolic processes can also alter the isotopic value of DIC.

Production of CO_2 by heterotrophic respiration may result in isotopic depletion as the $\delta^{13}C$ value of CO_2 produced will be similar to that of the source organic matter. Conversely, photosynthetic uptake of CO_2 may result in isotopic enrichment of DIC due to discrimination against C^{13} relative to C^{12} (McKenzie 1985; Hellings et al. 2001).

The primary objective of this study was to investigate the importance of groundwater carbon to floodplain spring foodwebs. This study was conducted in two parts. Firstly, an investigation of multiple sites along five spring streams was made to determine the relative importance of groundwater carbon to food-webs. This was followed by a whole stream manipulation of a further five springs to investigate the relative effects of out-gassing and photosynthesis on the longitudinal gradient identified in part one. Floodplain springs represent discrete ecotones between aquatic, subterranean and terrestrial ecosystems. As such, they provide model systems from which floodplain carbon cycling at multiple spatial scales, and across less discrete boundaries (e.g., diffuse groundwater up-wellings beneath main channels of flood-plain rivers) may be understood.

Methods

Study area

All spring streams, except for one on the West Coast, were located within the braided floodplains of high country catchments in the Canterbury region, South Island, New Zealand, at altitudes between 515 and 1000 m a.s.l (Figure 1). The area lies to the east of the main alpine spine of the South Island and occupies an orographic rain "shadow" produced by the prevailing "westerly" air flow. Consequently, whilst study sites and surrounding terrestrial habitats may experience considerable aridity, the alpine sourced rivers of which they are a part are subject to frequent, large and unpredictable flooding (Winterbourn 1997). Braided rivers are a product of this volatile hydrological regime and the friable nature of their lithologically unstable catchment bedrock (Gray & Harding 2007).

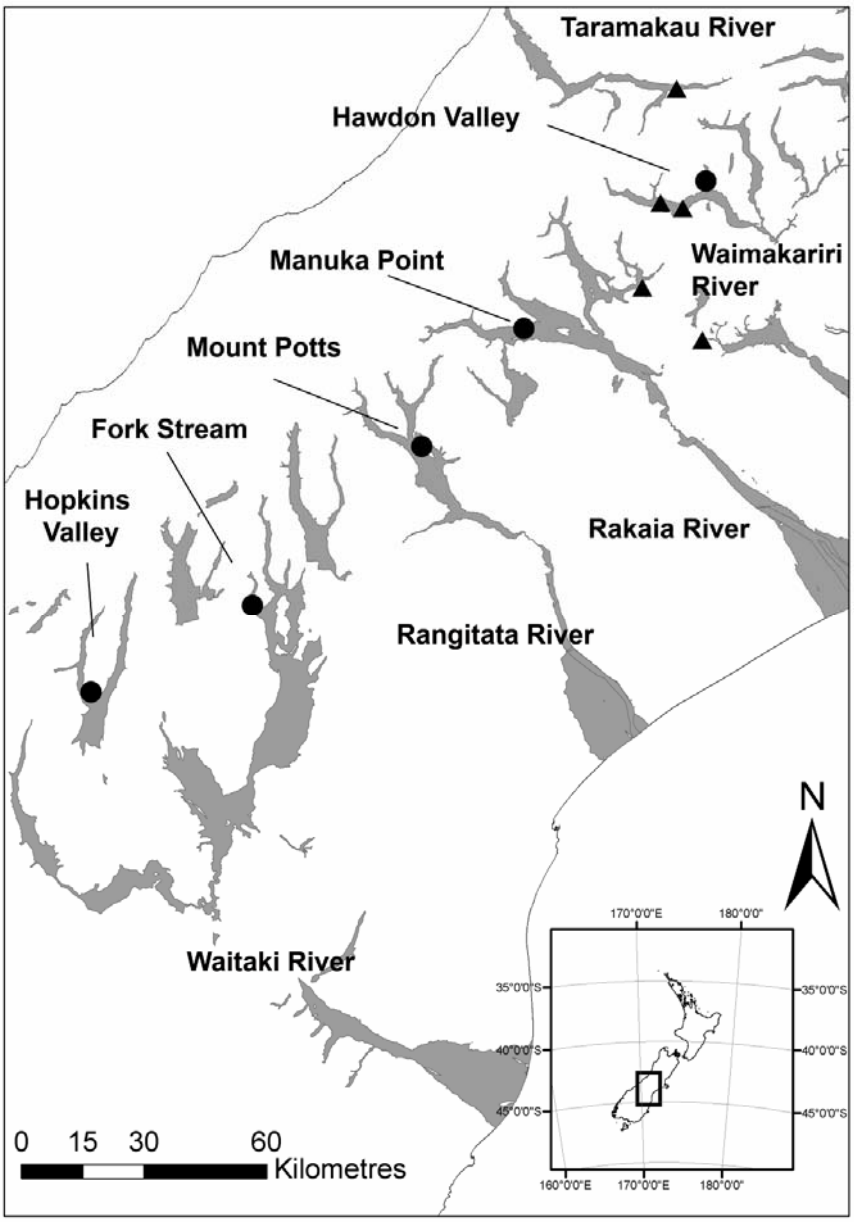

Figure 1. Location of the five spring streams included in the initial survey during September 2008 (closed circles). Springs used in the whole stream manipulation of out-gassing and photosynthesis during April 2009 (closed triangles). Symbols are superimposed on outlines of major river floodplains. Inset: location of map extent in New Zealand.

Site selection

Longitudinal survey

Five spring streams, arising on the floodplains of braided river beds were used to measure the response of stream ecosystems to groundwater carbon inputs. The streams were

located in the Hawdon valley, 2km upstream of the Sudden Valley Stream confluence, at 600m a.s.l; at Manuka Point in the Rakaia valley, at 600m a.s.l; at Mount Potts in the Rangitata Valley, 550m a.s.l; below Mt Joseph in the Fork Stream, a tributary of the Tekapo River, 1000m a.s.l and below Mt Glen Lyon in the Hopkins Valley, 600m a.s.l. (Figure 1). Five sampling sites were arranged along each stream at distances of 0, 6, 36, 216 and 1296 m from the up-welling source. The streams flowed for at least 1.5 km from their source through tussock grassland and across the unvegetated stony floodplains of their parent rivers. No forest or bush patches were present and no streams were in close proximity to swamps or likely sites for methanogenesis or sulfur bacteria which might have depleted $\delta^{13}C$ DIC (Jones & Mulholland 1998; Doi et al. 2006). Streams were sampled on sunny days with light breezes and so these variables should not unduly affect in-stream processes. This study was conducted in September 2008.

Whole stream manipulation

Five separate spring streams were chosen for the manipulation of out-gassing and photosynthesis, using the same criteria as described for the survey. In each stream a reach of 36m from the source was used and each spring had no inflowing tributaries within this reach. These streams were located within the Rakaia, Waimakariri and Taramakau river floodplains (Figure 1). The manipulation was carried out in April 2009.

Sample collection

Water chemistry

For the longitudinal study single grab water chemistry samples/data were collected at each of the five longitudinal sites. Water samples for the analysis of DIC ($\delta^{13}C$ and concentration) were collected in autoclaved 250 ml, Nalgene bottles from well-mixed areas of the stream during mid-morning through mid-afternoon. Bottles were rinsed three times in stream water and filled underwater ensuring that no head space remained in the bottle. Samples were immediately put on ice, in the dark, and returned to the laboratory within 24 hours and refrigerated. Samples were couriered on ice to the Geological and Nuclear Sciences Stable Isotope Laboratory, Wellington, stored in a refrigerator for 5 days at $4^{o}C$, before analysis. The whole stream manipulation used a different method for

the measurement of DIC. Vacuum sealed 12 ml exetainers were opened beneath the surface of the water. After filling, lids were replaced and vials were checked for gas bubbles. They were then kept on ice before the addition of a single drop of saturated sodium azide and shipping to the UC Davis stable isotope laboratory for analysis. Details of the specific analytical techniques for DIC are available at http://stableisotopefacility.ucdavis.edu/, (accessed July 2009), but are broadly similar to those outlined by Spotl (2005).

Water samples for measurement of dissolved organic carbon (DOC) concentration for each site during the longitudinal study were collected in 250 ml plastic bottles, held on ice in the dark and returned to the laboratory within 24 hours. Samples were stored in a refrigerator at 4 ^{o}C, and processed within 2 days. DOC concentration was estimated using the spectrophotometric method of Collier (1987). Temperature (^{o}C) and conductivity ($\mu S_{25} cm^{-1}$) were measured with a calibrated Oakton conductivity/ temperature 10 meter and dissolved oxygen with a YSI 550 meter. pH was measured with a Solstat FET pH meter and glass electrode with re-calibration before each measurement.

Food-web components

Samples of aquatic bryophyte, macrophyte and filamentous algae for isotopic analysis were collected from mid-stream to reduce the likelihood that plants had been exposed to the atmosphere during periods of low flow. Emergent macrophytes and bryophytes were not collected. Diatom layers were scrubbed from at least four stones using a tooth brush and all invertebrates or plant detritus removed. Aquatic invertebrates were collected with a kick-net. Where possible I collected the leptophlebiid mayfly *Deleatidium* spp. and hydrobiid snail *Potamopyrgus antipodarum* (primary consumers), predatory Hydrobiosid caddis larvae, *Hydrobiosis* and *Psilochorema*, and the predatory stonefly *Stenoperla*. Where these taxa were not available other members of the appropriate consumer guild were collected. Fish were captured with a Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, N.Z.) with 300–600 V pulsed DC (pulse width ~ 3 ms, 60 pulses s^{-1}). All fish in these streams are predators. The native galaxids (*Galaxias*

paucispondylus, *G. vulgaris*) were collected in preference but, where absent, salmonids (*Oncorhynchus mykiss*, *Salmo trutta*,) or bullies (*Gobiomorphus breviceps*) were taken. Lastly, we collected riparian fishing spiders (*Dolomedes aquaticus)* from each site as these spiders have been shown to derive over 90% of their diet from larvae or adults of aquatic insects (Williams 1979). Most spiders were found beneath overhanging tussocks directly adjacent to the stream. All organic samples were held on ice in the dark, returned to the laboratory within 24 hours and frozen at -20^{o}C.

At each site a range of physico-chemical parameters was measured. Stream size was assessed across three transects by measuring wetted width, depth and velocity. Between sites percentage macrophyte cover was estimated visually. Proportion of pool, riffle and run between sites was also visually estimated. Altitude was measured using a Trimble Recon GPS XC unit and used to calculate average slope between sites. Finally, wind speed and air temperature were recorded adjacent to each site.

Whole stream manipulation

To test the relative contributions of out-gassing and photosynthetic uptake of CO_2 on $\delta^{13}C$ of DIC I performed a fully factorial manipulation in five springs. Initially, water chemistry measurements and water samples were collected from the source of each stream and at 6, 16 and 36 m downstream. In order to inhibit out-gassing, but not photosynthesis, we laid a continuous sheet of transparent polythene over the entire 36m length of stream. Once a satisfactory seal had been achieved and all gas pockets had been removed from beneath the sheet, the stream was left for 1 hour for CO_2 concentrations to reach a new steady state without atmospheric interference, and sampling was repeated. The polythene sheet was then removed and all macrophytes, bryophyes and algal mats were removed; substrates with obvious diatom layers were either removed or inverted. The streams were then left for a further hour before re-sampling, after which the polythene sheeting was replaced on the de-vegetated streams, which were left once again, before final water chemistry and samples were taken. After each sample collection we estimated residence time of water in each reach using a fluorescein dye tracer. Due to the nature of the experimental design and the availability

of suitable stream reaches it was not possible to randomize the sequence in which treatments were applied.

Sample preparation and analytical techniques

Bryophyte, macrophyte and filamentous algae were rinsed and contaminant material removed under 40X magnification. Digestive tracts of all aquatic invertebrates and riparian spiders were removed. Although the cephalothorax and leg coxae of *D. aquaticus* may contain stored food materials, Collier et al. (2002) found no significant difference in $\delta^{13}C$ values between them and legs minus coxae, therefore we combined all lower leg and cephalothorax material in samples. Snail shells were removed prior to isotope analysis. This can be achieved either through manual extraction of soft tissues or by dissolving the shell in HCL. The two techniques were compared and no effect was found of HCL on $\delta^{13}C$ values ($p = 0.993$), however, $\delta^{15}N$ values for material treated with HCL were significantly lower ($p = 0.01$). Therefore, I used the more labor intensive manual extraction. All organic material was then dried at 45^{o}C for at least 48 hrs before being ground with a mortar and pestle. Because endogenous lipids have more depleted $\delta^{13}C$ values than other major compounds (i.e. proteins and carbohydrates) in both plant and animal tissues this presence can affect conclusions drawn from $\delta^{13}C$ analyses in food web studies (Logan et al. 2008). Therefore, lipids were extracted from all samples as described by Logan et al. (2008). Samples were then re-dried at 45^{o}C for at least 48 hrs and frozen at -80^{o}C prior to isotope analysis.

Estimations and statistical analyses

Excess PCO_2

The partial pressure of carbon dioxide (PCO_2) in water samples was estimated using the relationship given by Doctor et al. (2008):

$$\frac{C_T \alpha_0}{K_H} = PCO_2 \qquad (1)$$

where C_T is the total DIC concentration (mol C l^{-1}) in the sample, α_0 is the ionization fraction between CO_2 and H_2CO_3 (Stumm & Morgan 1981) and K_H is the Henry's law equilibrium constant for CO_2 in water. Because K_H is temperature dependent, its value was estimated from the temperature of the stream at the time of sample collection using the relationships provided in Telmer & Veizer (1999). Note however, that the values of K_1, K_2 (used to estimate α_0) and K_H should actually be pK (raised to the log base 10) to provide parts per million by volume (ppmV) values for PCO_2. Excess PCO_2 ($ePCO_2$) is the ratio of the calculated value of PCO_2 in the sample to that of the atmosphere which was assumed to be 387 ppmV. The $ePCO_2$ value is a multiplicative factor of the atmospheric concentration such that an $ePCO_2$ value of 10 is 10 times greater than the atmospheric concentration (Doctor et al. 2008).

Food-web components and water chemistry

Relationships between water chemistry variables, $\delta^{13}C$ of DIC, $\delta^{13}C$ of the various food-web components and distance downstream were assessed using mixed effects linear models. Mixed models were used to remove variation contributed by the random, higher level effects, before assessing patterns due to fixed variables. To test for homogeneity of slopes between significant food-web components and DIC we used a mixed effects linear model ANCOVA. The $\delta^{13}C$ value of filamentous algae and distance were $\log_{10}$ transformed to improve normality and homogeneity of variances. Stream was the random effect. Analyses were conducted in R using the package "lme4" (R Development Core Team 2007).

Downstream patterns of DIC

To test the importance of different physico-chemical variables on downstream enrichment of $\delta^{13}C$ DIC we used multiple regression analyses. $\delta^{13}C$ DIC was standardized within each stream to the "at source" value to remove the effect of between stream variability. Initial correlations between predictor variables within each stream revealed weak to moderate collinearity which can cause estimates of parameters to be unstable and produce artificially large variances (Quinn & Keough 2002). Collinearity can be removed from a data set by removing variables considered to be measuring similar

phenomena, however it was our goal to test the independent effects of these correlated variables. Hierarchical partitioning allowed the contribution of each predictor to the total explained variance of a regression model, both independently and in conjunction with the other predictors, to be calculated for all possible candidate regression models (Quinn & Keough 2002). We performed hierarchical partitioning using r^2 as the "goodness of fit" measure. Significance was assessed with *Z*-scores after 999 randomizations, and analyses were conducted with "hier.part" and "rand.hp" functions (Mac Nally & Walsh 2004) in R (R Development Core Team 2007). To test further for the independent significance of individual variables whilst controlling for the stream effect we also used a mixed effects general linear model on non-standardised data. Stream was the random effect and variables were rejected based on AIC numbers (reject if change <2). This analysis was also conducted in R using the package "lme4" (R Development Core Team 2007). The following transformations were made; slope (degrees), $ePCO_2$ (ppmV) and wind speed (m/s) were $\log_{10}$ transformed, whilst upstream percentage macrophyte cover and percentage riffle were arcsine square root transformed.

Whole stream manipulation

The effect of "whole stream" manipulations on $\delta^{13}C$ of DIC were assessed using mixed effects linear models. $\delta^{13}C$ of DIC, standardised to the value at source of each stream, was used as the response to control for the effect of variable stream source values. The change in residence time of water along each site as a result of macrophyte removal was used as the stream level random factor. Significant differences during mixed effects linear model simplification were identified using ANOVA and *p* values. The final model was fit by REML.

Results

Longitudinal study

All five spring streams were characterised by broadly similar physico-chemical conditions. Discharge increased rapidly from the initial upwelling, but in most cases had begun to level off after 200 m whereupon significant groundwater inputs were minor (Figure 2). The exception was the Mount Potts stream which was joined with a large stream also draining a groundwater upwelling zone at 800 m.

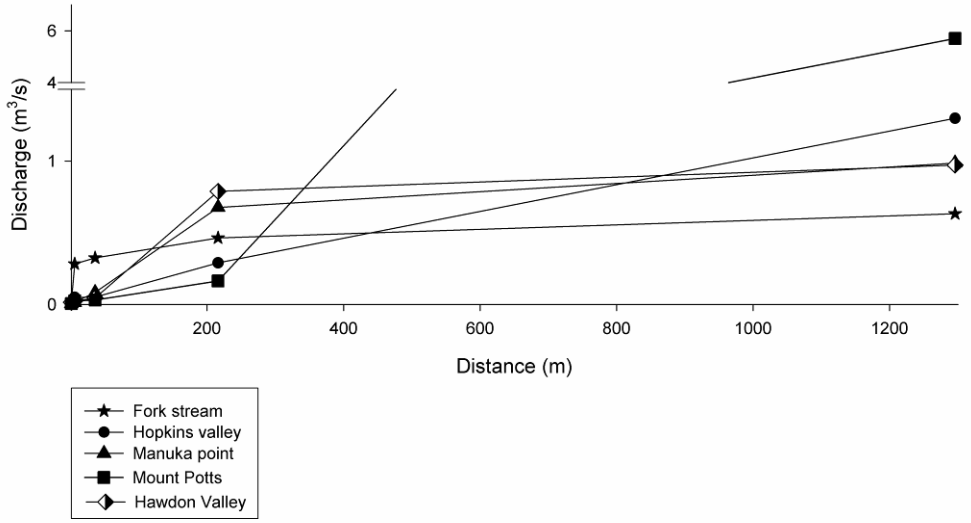

Figure 2. Discharge of five spring creeks over 1.296 km at sampling sites during September 2008.

Table 1. Physico-chemical conditions along the five spring streams sampled in September 2008. Hawdon Valley sites are included in this data set. * pH values are only shown as a range. Up-stream macrophyte and riffle values are for the stream reach directly above each site.

	All sites		Source	Lowest site
	Mean	Range	Range	Range
pH	*	7.0 - 8.0	7.0 - 7.5	7.6 - 8.0
Temperature (^{o}C)	7.9	6.4-11.2	6.4- 9.0	7.3-11.2
Conductivity ($\mu S_{25} cm^{-1}$)	57	39-97	41-65	39-80
Dissolved oxygen (% saturation)	95	76-112	76-94	101-108
DOC (gm^{-3})	2.18	0-3.2	0-2.6	1.9-3.2
Average slope (degrees)	1.6	0-13	0	0.37-1
Up-stream macrophyte cover (%)	31	0.5-90	15-90	0.5-1
Up-stream riffle (%)	37.0	0-90	0-5	30-90
Air temperature (^{o}C)	15.2	9.1-20.3	na	na
Wind speed (ms^{-1})	5.0	0.5-27	na	na

Water temperature at spring sources (6.4-9 ^{o}C) was approximately equal to the annual average air temperature (Gray et al. 2006) and pH was circumneutral. However, both temperature and pH increased logarithmically downstream (Figure 3). Conductivity was low and fairly constant (range 39-97 $\mu S_{25} cm^{-1}$) along the 1.2 km reaches (Table 1). Dissolved oxygen was not saturated at spring sources (range 76-94 %) but, became

saturated downstream. DOC concentrations were very low, and at some spring sources were undetectable (< 1.6 g m^{-3}). All streams flowed across river flats for their entire length and therefore slopes were slight. Spring sources were typically pools with high percentage cover of macrophytes. However, macrophyte cover rapidly declined downstream as current velocity increased. Unfortunately, water samples from Hawdon valley springs were partially frozen during storage resulting in a gas head formation within the vessel, and therefore could not be used to analyse DIC, they are subsequently omitted from a number of analyses and plots. The relationship between distance and DIC concentration (mmoles/kg) was highly influenced by an outlier, the lower site on the Hopkins valley stream (Figure 3). Before exclusion of this data point the relationship was not significant (p=0.28), however after the point is removed there is significant logarithmic downstream decline in DIC concentration (p = 0.003). Excess partial pressures of carbon dioxide ($ePCO_2$) ranged from 2 - 7 times atmospheric pressure at spring sources, but were invariably <1.5 at the downstream site. The average $\delta^{13}C$ value of DIC at spring sources was -12.7‰ suggesting that DIC was a combination of C_3 derived CO_2 and HCO_3^- derived from mineral dissolution by carbonic acid. DIC became more enriched in ^{13}C downstream (Figure 3). Although the general pattern was observed in all streams, absolute upstream and downstream $\delta^{13}C$ values varied from -15.6‰ to -12.2‰ at sources, to -12.5‰ - 9.0‰ at 1296 m downstream.

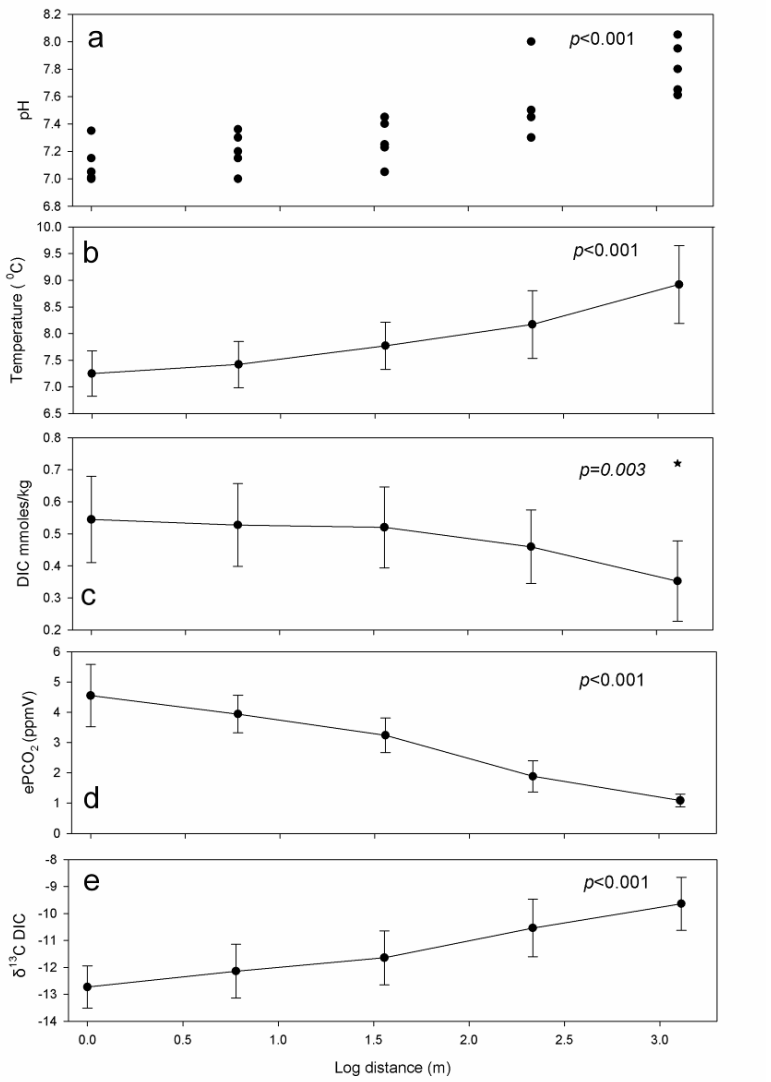

Figure 3. Downstream gradients in a) pH, b) temperature, c) DIC concentration, d) excess partial pressure of CO_2 ($ePCO_2$) and e) $\delta^{13}C$ DIC from five spring streams (mean ± 1 S.E.). Means and error bars were not calculated for pH. The Hawdon valley DIC concentration, $ePCO_2$ and δC^{13} DIC data are excluded. The excluded outlier of DIC concentration from the lower Hopkins valley site is shown on plot c) (*). Significance of the relationship between log distance and water chemistry variables are shown after testing with mixed effects linear models with stream as the random effect.

The $\delta^{13}C$ of diatoms, moss, primary consumers, invertebrate predators and fish all showed a significant positive relationship with $\delta^{13}C$ DIC (Figure 4). Filamentous algae was highly influenced by an outlier (data point included p =0.4), but excluding this point resulted in a significant positive relationship (p <0.001). The only food-web components

not related to $\delta^{13}C$ DIC were macrophytes and riparian spiders. Thus, multiple trophic levels of the spring food-web tracked the rapid downstream enrichment of $\delta^{13}C$ DIC.

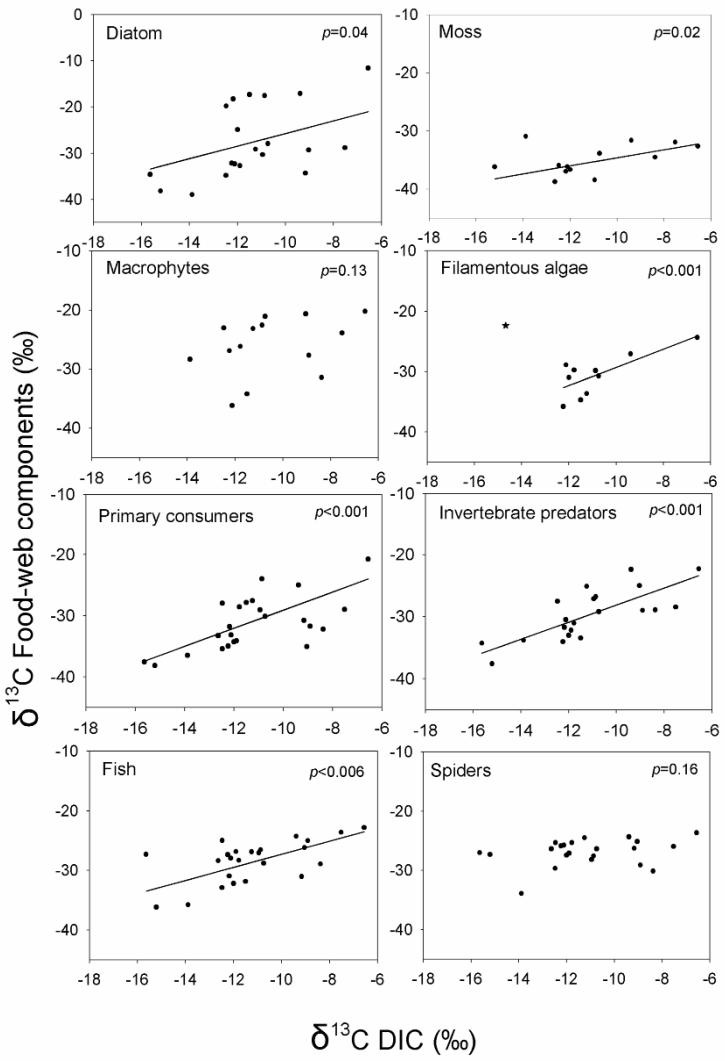

Figure 4. Relationships between the $\delta^{13}C$ of food-web components sampled along five spring streams and $\delta^{13}C$ of DIC. Plots are actual data, but trend lines and *p* values are derived from mixed effects linear models with stream as random factor. The outlier in the plot of filamentous algae versus $\delta^{13}C$ of DIC is shown (*). Mixed effects ANCOVA indicated no significant difference between the slopes of each significant line (d.f., 11, X^2=5.779, p=0.2).

To identify the drivers of $\delta^{13}C$ DIC enrichment multiple regression analysis was used. Some physical predictors were inter-correlated, but collinearity was weak to moderate (VIF = 1.5-3.2). Percentage upstream cover of macrophytes was significantly correlated with ePCO_2 (r = 0.621) and the percentage of riffle habitat (r = -0.654). Hierarchical

partitioning, using standarised data identified both macrophyte cover and ePCO_2 as having significant independent effects on DIC $\delta^{13}C$ (Table 2).

Table 2. Results of hierarchical partitioning analysis of six physico-chemical predictors of $\delta^{13}C$ DIC. Bold type indicates significant ($p < 0.05$) independent variance after 999 randomisations of the hierarchical partitioning analysis. Goodness of fit measure was r^2. Hawdon valley data were excluded from this analysis.

	Independent	Joint	Total
Slope (degrees)	0.018	-0.002	0.017
ePCO_2	**0.182**	0.269	0.451
Macrophyte cover (%)	**0.282**	0.342	0.624
Riffle (%)	0.132	0.222	0.353
Air temperature (^{0}c)	0.017	0.003	0.020
Wind speed (ms^{-1})	0.120	0.146	0.267

Overall, macrophyte cover explained the greatest amount of the independent variance of the six variables considered. This analysis was repeated using actual data with a mixed effects linear model and only macrophyte cover (p=0.005) and ePCO_2 (p<0.001) were found to be significant. However, the AIC differential in explanatory power due to removal of a variable was greater for ePCO_2 (12.03) than macrophyte cover (5.84) which is inconsistent with the hierarchical partition.

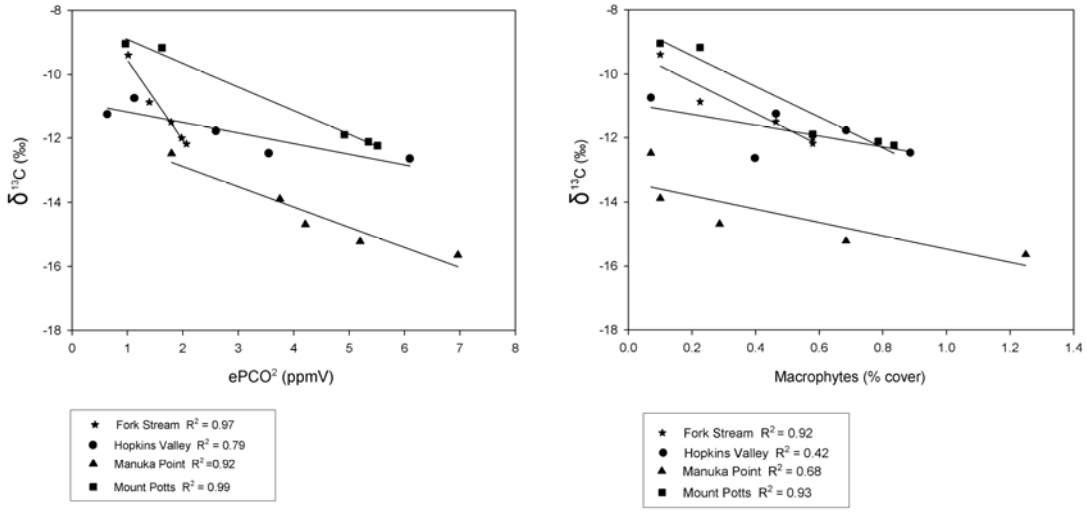

Figure 5. Relationships between the $\delta^{13}C$ signature of DIC, excess partial pressure of carbon dioxide and percentage upstream cover of macrophytes (arcsine square root transformed) in individual streams (actual data). The r^2 values for individual regressions are shown below each plot. Hawdon Valley data are excluded.

Plots of ePCO_2 and up-stream macrophyte cover against DIC $\delta^{13}C$ in individual streams are shown in Figure 5. Slopes and range of the regression lines for ePCO_2 and DIC $\delta^{13}C$ were similar in all streams apart from Fork stream. Isotopic enrichment of DIC along Fork stream was comparable to that at other sites, but ePCO_2 at the source was only twice that of the atmosphere, and only decreases by a single unit over 1.2 km. Slopes and ranges of regressions lines for macrophyte cover and DIC $\delta^{13}C$ were broadly similar. Hierarchical partitions using standarised data would have been highly influenced by the homogeneity of slopes, however r^2 squared values for individual regression lines are consistently greater between ePCO_2 and DIC $\delta^{13}C$, than macrophyte cover and DIC $\delta^{13}C$. This would have been more influential on a mixed effects linear model using actual data, thus the contrary result. Unfortunately these analyses are not able to disentangle the effects of macrophyte cover and ePCO_2 on downstream patterns in DIC $\delta^{13}C$ due to co-linearity.

Whole stream manipulation of out-gassing and photosynthesis

After controlling for between stream effects (standardisation) and within stream changes in residence time due to the manipulation (random factor) I observed a negative shift in $\delta^{13}C$ DIC due to both stream out-gassing and photosynthetic uptake of CO_2 (Figure 6; Table 3). However, within the initial 36 m of the spring streams only out-gassing had a significant effect on $\delta^{13}C$ DIC.

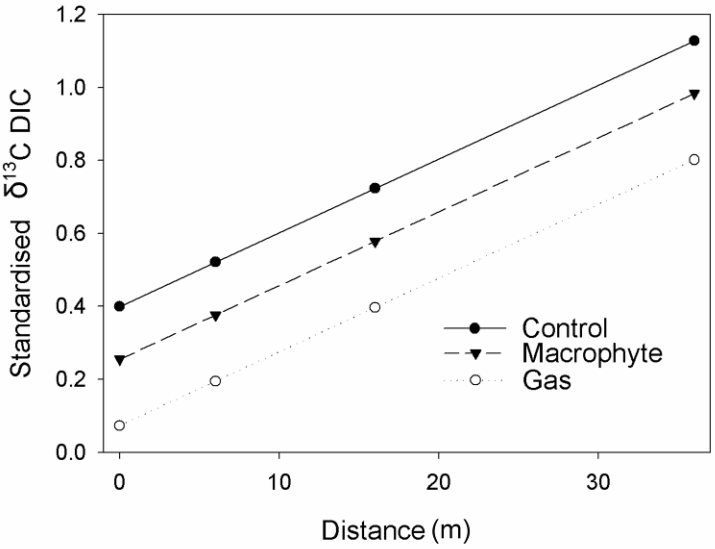

Figure 6. The relationship between $\delta^{13}C$ DIC, standardised to an identical source value, and distance downstream before and after whole stream manipulations of out-gassing and photosynthetic uptake in five spring streams derived from mixed effects linear models.

Table 3. Linear mixed-effects model tested with maximum likelihood estimation to investigate the main and interactive effects of the prevention of out-gassing and removal of macrophytes (fixed categorical variables) on the downstream shift in $\delta^{13}C$ of DIC. This analysis accounted for stream specific change in residence time of water due to the removal of macrophytes (random effect) and the stream specific variation in $\delta^{13}C$ of DIC at source (response = standardised $\delta^{13}C$ DIC). We used model simplification to estimate the Chi square (X^2) statistic and its significance level (p value) for each fixed effect and their interaction. Var. = variance explained by the random block effect. P values <0.05 are indicated in bold.

Predictors	Type	var.	X^2	df	p value
Stream	Random	0.22463			
Out-gasssing	Treatment		6.7641	2	**0.03**
Macrophyte removal	Treatment		2.0492	2	0.35
Distance	Covariate		13.143	1	**<0.001**

Out-gassing:macrophyte	Treatment interaction	1.1533	3	0.76

Discussion

Results of this study show that biological communities in floodplain spring streams are highly dependent upon inorganic carbon originally derived from terrestrial vegetation in the greater catchment. This carbon is converted from organic to inorganic forms within soils and groundwater, thereby becoming available to aquatic consumers. Due to high concentrations of $\delta^{13}C$ depleted carbon in groundwaters I observed strong biogeochemical fluxes within spring streams, i.e. stream to atmosphere fluxes, which appear to be the result of the physical process of out-gassing.

Drivers of downstream $\delta^{13}C$ enrichment

A number of stream studies have suggested that carbon (isotope) exchange with atmospheric CO_2 ($\delta^{13}C$~ -8‰) may be partially responsible for downstream enrichment of $\delta^{13}C$ DIC values (Taylor & Fox 1996; Yang et al. 1996; Atekwana & Krishnamurthy 1998; Amiotte-Suchet et al. 1999; Aucour et al. 1999; Karim & Veizer 2000; Helie et al. 2002; Mayorga et al. 2005; Kanduc et al. 2007). However, these studies focused on processes in large rivers and compared headwaters with lower reaches. They have shown that headwaters were depleted in $\delta^{13}C$ DIC relative to lower reaches. Passive exchange of CO_2 between stream and atmosphere would be expected to show a linear relationship with distance downstream. However, in my study the change in $\delta^{13}C$ DIC showed a logarithmic relationship with distance downstream, suggesting that mixing with atmospheric CO_2 did not have a significant effect on $\delta^{13}C$ DIC in the first ~1.2 km of these spring-fed streams. Doctor et al. (2008) pointed out that passive exchange between stream water DIC and atmospheric CO_2 can only occur once the partial pressure gradient between water and gas has reached equilibrium, (i.e. an ePCO_2 of 1). Therefore, when a chemical drive for CO_2 evasion exists (ePCO_2 >1) CO_2 out-gassing will prevent enrichment due to invasion of atmospheric CO_2. In the groundwater dominated streams in this study partial pressures of CO_2 were in excess of atmospheric pressure at the majority of sites. Only the lower sites on the Hopkins Valley and Mt Potts streams had reached chemical equilibrium with the atmosphere and might therefore have begun to

exhibit passive exchange of CO_2 with the atmosphere. In both streams $\delta^{13}C$ DIC was depleted relative to the atmosphere (-11.2‰ and -12.45‰ respectively) suggesting that any further downstream (below ~1.2 km) enrichment might be due in part to mixing between stream DIC and atmospheric CO_2.

Doctor et al. (2008) reported a positive shift in $\delta^{13}C$ DIC between 1 and 4‰ over tens of metres downstream from a spring source and attributed this shift to out-gassing of CO_2, due to the absence of any significant photosynthetic activity. In contrast, Hellings et al. (2001) observed seasonal enrichment in the order 4 - 7‰ of $\delta^{13}C$ DIC in a highly polluted estuary and attributed it to CO_2 drawdown by photosynthesizing phytoplankton. Numerous other studies of freshwater rivers and lakes, as well as brackish and saline habitats, have observed a positive correlation between photosynthesis and DIC $\delta^{13}C$ (Barth & Veizer 1999; Bontes et al. 2006; Wachniew 2006; Trojanowska et al. 2008).

The spring sources in this study were dominated by the macrophyte *Callitriche stagnalis*, which forms a thick mat covering the water surface. Madsen (1991) described *Callitriche* in Danish streams which depended upon CO_2 over-saturation for a sufficient supply of DIC. This tendency might explain this plant's affinity for up-welling zones. In contrast, other macrophyte taxa use morphological and physiological adaptations, such as finely dissected leaves (*Myriophyllum* sp.), to increase efficiency of carbon uptake or use of C_4 or CAM photosynthetic pathways (Madsen 1991). Results from Fork stream in this study suggested an important role which macrophytes might play in regulating $\delta^{13}C$ DIC enrichment, as enrichment equivalent to that seen in the other streams took place in the absence of a comparable gradient in ePCO_2. Interestingly no *Callitriche* was seen in the Fork stream, possibly due to its low ePCO_2, although a considerable cover of filamentous algae, bryophytes, and *Myriophyllum* sp. was present.

The whole stream manipulation of both out-gassing and photosynthetic uptake of dissolved CO_2 indicated that close to spring sources out-gassing is the major driver of downstream $\delta^{13}C$ enrichment. The incorporation of groundwater carbon into stream food-webs indicates that photosynthetic uptake of CO_2 occurs, but this effect is

overwhelmed by that of out-gassing. Hendy (1971) suggested that isotopic fractionation of DIC due to CO_2 loss by out-gassing becomes significant only when ePCO_2 is greater than twice that of the atmosphere and these results are in accordance with this. During the manipulation ePCO_2 ranged from 4.5 to 8.9 and at all points in the experimental reach there would have been a strong chemical drive for CO_2 evasion. Further downstream, below the manipulation reaches, where ePCO_2 approaches equilibrium, macrophyte, bryophyte and algal cover will also be reduced. However, it is quite possible that photosynthetic uptake could have a significant influence on CO_2 levels and $\delta^{13}C$ DIC as suggested by the diel shift in ePCO_2 observed by Finlay (2003) in the South Fork Eel River.

Primary producer response

The primary food of the dominant consumers in these springs (e.g. the mayfly *Deleatidium* and snail *Potamopyrgus*) is the diatom film (Winterbourn 2000) which showed a strong relationship to $\delta^{13}C$ DIC. Mosses and filamentous algae also showed a significant relationship with $\delta^{13}C$ DIC, but are unlikely to have been consumed directly by any of the invertebrates used in this study (Death 2000). However, bryophytes and filamentous algae are an integral part of the overall food-web (Suren & Winterbourn 1991; Winterbourn 2000). However, macrophytes did not adhere to this trend. Algae are known to vary widely in $\delta^{13}C$ between species, water velocity, and CO_2 availability (Finlay et al. 1999; Finlay 2001) and similar results have been obtained for aquatic macrophytes. Still-water macrophytes have been shown to have markedly more enriched $\delta^{13}C$ values than individuals of the same species in flowing water (France 1995). The generally low water velocity in spring sources compared to downstream reaches means velocity might have contributed to the relative invariance of macrophyte $\delta^{13}C$ values across a broad range of $\delta^{13}C$ DIC. Further, $\delta^{13}C$ enrichment of plant material in spring sources may have occurred due to exposure of macrophytes to the atmosphere during periods of low flow.

Food-web response

A highly revealing result was that food-webs of the spring streams were tightly coupled to the downstream flux in $\delta^{13}C$ DIC. Primary consumer, predatory macroinvertebrates and fish showed particularly strong relationships with DIC. The strong relationship for fish suggests they move around little within these streams, or their $\delta^{13}C$ values adjusted rapidly. The lack of a significant downstream enrichment of riparian spider $\delta^{13}C$ is contrary to the assumption that *Dolomedes aquaticus* derives the majority of its diet from aquatic sources (Williams 1979). Fishing spiders may be less reliant on aquatic prey around heavily vegetated streams such as these spring sources. Furthermore, there may be seasonal shifts in use of aquatic versus terrestrial prey relating to the relative abundance of each. Peak emergence times for common aquatic insects in other streams in this part of New Zealand are during late spring and summer (Winterbourn & Crowe 2001), whereas our collections were made in early spring (September).

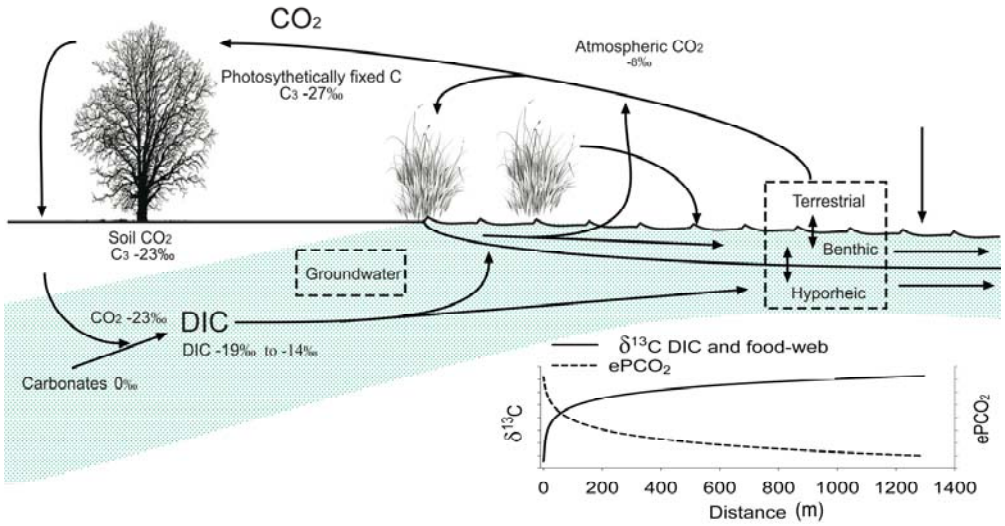

Figure 7. Conceptual diagram of the major pathways, forms and isotopic values of carbon that influence autochthonous spring ecotones in a braided river floodplain. δ^{13} values of different carbon forms are shown and dashed boxes represent food-webs (see chapter 5). Inset: relationship between $\delta^{13}C$ of DIC and food-web components (solid line) and ePCO_2 (dashed line) with distance from spring source.

Floodplain carbon cycling

Results of this study indicate a strong dependence of floodplain spring ecosystems on groundwater carbon. More importantly in terms of whole ecosystem processes it illustrates aspects of the carbon cycle within floodplains and catchments that link terrestrial, subterranean and aquatic components (Figure 7). The $\delta^{13}C$ of atmospheric carbon is approximately -8‰. Photosynthesis by terrestrial C_3 plants depletes this carbon to ~ -27‰ and this carbon subsequently becomes incorporated into soils. Soil respiration produces CO_2, with a similar isotopic signature to its parent material, which enters groundwater resulting in high concentrations of DIC and high partial pressures of CO_2 relative to the atmosphere. Upon discharge into surface streams this DIC is used by macrophytes and algae for photosynthesis or released to the atmosphere by out-gassing. Fractionation of carbon during aquatic photosynthesis results in further depletion in ^{13}C (reducing $\delta^{13}C$ by about 20‰) before carbon is incorporated into the aquatic food-web. The double depletion of $\delta^{13}C$ by photosynthesis in terrestrial plants and subsequently aquatic plants results in the transmission of highly negative values through the entire stream food-web. The rapid flux in DIC out of the stream water by out-gassing and respiration releases the CO_2 back to the atmosphere to complete the cycle.

Further research and implications

Depending on residence time and rates of microbial activity, groundwater is generally supersaturated with CO_2. Therefore, there is the potential for primary productivity in spring streams to be enhanced relative to streams with CO_2 partial pressures at equilibrium with the atmosphere. If this proves to be the case, groundwater carbon inputs to surface-flowing streams can be described as a subsidy between ecosystem compartments, or more correctly, enhanced productivity constitutes an emergent property of floodplain carbon cycling. Thus, the cycling of carbon between terrestrial, subterranean and aquatic system components, with concomitant transformations between organic and inorganic forms and changes in concentration, increases overall reach scale productivity. The emergent effects of these linkages will be most pronounced when they connect sub-systems that are carbon limited. Hydrologically mediated biogeochemical linkages have mainly been studied at small scales within the confines of the active river channel. For example, Valett et al. (1994) describe enhanced post-flood algal growth due

to upwelling nutrient rich hyporheic water, and Jones et al. (1995) observed rapid post-flood recovery of hyporheic respiration due to down-welling water rich in labile dissolved organic carbon. An important advance would be to extend our understanding of linkages to larger spatial scales and to complete (whole) cycles of carbon and other potentially limiting nutrients. Such research would complement the telescoping ecosystem model of Fisher et al. (1998) whereby the river is viewed as a nested array of cylindrical components with varying nutrient/energy spiral lengths which increase due to disturbance and decrease during succession. Nutrient processing in more lateral components, e.g. riparian zones or groundwater, show greater resistance to floods, but lower resilience (post-flood recovery) and vice versa. Most importantly cross-linkages between adjacent systems result in greater resilience of the whole system, enhanced diversity and productivity.

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Chapter 5: Riparian vegetation mediates stream community use of carbon: invertebrate response to successional change in a braided river floodplain spring stream

Grassland spring source (top) and forest spring stream in the Hawdon Valley, Canterbury, South island. Note thick beds of the macrophyte *Callitriche stagnalis* and bryophytes in the forest spring stream.

Abstract

The fluxes of energy, materials and individuals between stream and landscape are profoundly important to both systems, and to understand how streams function they need to be studied within their landscape context. In particular, forest streams have been shown to be intimately linked to terrestrial inputs of organic matter and open canopied streams to autochthonous energy sources. In autochthonous spring-fed streams the primary energy source may be inorganic carbon derived from respiration in soils. However, spring streams with dense riparian vegetation may not be able to fix groundwater carbon due to low light levels. In order to determine the differential importance of organic versus inorganic carbon sources I investigated stream food-webs in two adjacent floodplain spring streams with differing vegetation (one in forest and one in grassland). The $\delta^{13}C$ values of invertebrates in the grassland spring stream were depleted relative to local allochthonous materials (-28.8‰), suggesting a degree of dependence of the grassland spring stream invertebrate community on groundwater derived carbon. In contrast, invertebrates at the source of the forest spring stream ranged from -35‰ to -25‰ indicating use of both autochthonous and allochthonous carbon pathways. However, downstream the community became more depleted in $\delta^{13}C$ until all invertebrates showed values <-29‰, again indicating some dependence on carbon derived from groundwater. I also observed isotopic depletion of hyporheic taxa in the forest spring stream suggesting a reciprocal feedback of groundwater derived carbon back to the subsurface community after fixation in the benthos. In these floodplain springs riparian vegetation augmented rather than determined the carbon incorporated into food-webs and the dominant energy pathway appeared to be fuelled by inorganic carbon in groundwater. Overall, contrasting stream types contribute to high reach richness due to the interaction of successional diversity in the stream-riparian complex and up-welling groundwater.

Introduction

A critical advance in stream research has been the exploration of the "leakiness" of stream boundaries which indicated that lateral fluxes of energy between aquatic and terrestrial ecosystems can be profoundly important to both systems (Wallace et al. 1997; Power 2001; Baxter et al. 2005). Vertical exchange also occurs between a stream and both hyporheic and groundwater zones (Stanford & Ward 1988), but has been less intensively investigated. Stream systems are also influenced by material exported from up-stream such that downstream conditions are the cumulative product of the upstream catchment (Vannote et al. 1980). A greater understanding of how stream ecosystems are structured and function can be gained from studies that incorporate a broad landscape perspective, particularly when integrated into holistic models of ecosystem function (Fisher et al. 2004).

The ultimate basal resource for any biological system is carbon. The carbon used by a stream ecosystem has classically been separated into autochthonous and allochthonous sources. Autochthonous carbon is fixed by aquatic autotrophs from the inorganic carbon dissolved within stream water. Allochthonous carbon, in contrast, has been fixed into organic molecules by terrestrial plants prior to being added to the stream (a cross-boundary material flux) (Allen & Castillo 2007). Stream systems have been shown to be profoundly influenced by either the quantity of terrestrial input in forests (Fisher & Likens 1973; Wallace et al. 1997), or by light and nutrient availability in open canopied, autochthonous streams (Minshall 1978; Quinn et al. 1997; Allen & Castillo 2007). Whereas the pathways and in-stream dynamics of allochthonous carbon are well understood (Webster & Benfield 1986; Allen & Castillo 2007), sources of inorganic carbon supply to stream autotrophs are less well known (but see Finlay 2001; 2003). Within streams inorganic carbon availability is dictated by the balance between atmospheric diffusion, in-stream metabolism and, when present, groundwater inputs (Allen & Castillo 2007). Atmospheric diffusion exchange results in a shift in the CO_2 concentration of water towards that of the atmosphere (387 ppmV), whereas in-stream metabolism will either increase or decrease CO_2 concentration depending on the balance between photosynthesis (-ve) and respiration (+ve) (Fisher & Likens 1973). Finally,

groundwater is generally supersaturated with CO_2 due to soil respiration within the catchment (Dawson et al. 1995; Jones & Mulholland 1998).

Stable isotopes have revealed much detail about the sources and pathways of inorganic carbon, including groundwater carbon (Chapter 4) (Figure 1). Most carbon dissolved within groundwater is derived from the microbial breakdown of terrestrial organic matter and root respiration (Dawson et al. 1995), and might thus be considered to be part of the allochthonous contribution; fixation by terrestrial plants has resulted in its presence within groundwater. Additionally, in-stream decomposition of both terrestrial and aquatic organic materials may contribute to the pool of dissolved inorganic carbon, which in turn fuels the autochthonous food-web. So, whilst the basic dichotomy of allochthonous versus autochthonous is a useful construct for considering energy sources to streams, a more comprehensive model would identify carbon cycling and pathways across a range of scales, between sub-units within a watershed, and compartments within a stream (Fisher et al. 1998; Allen & Castillo 2007; Poole et al. 2008).

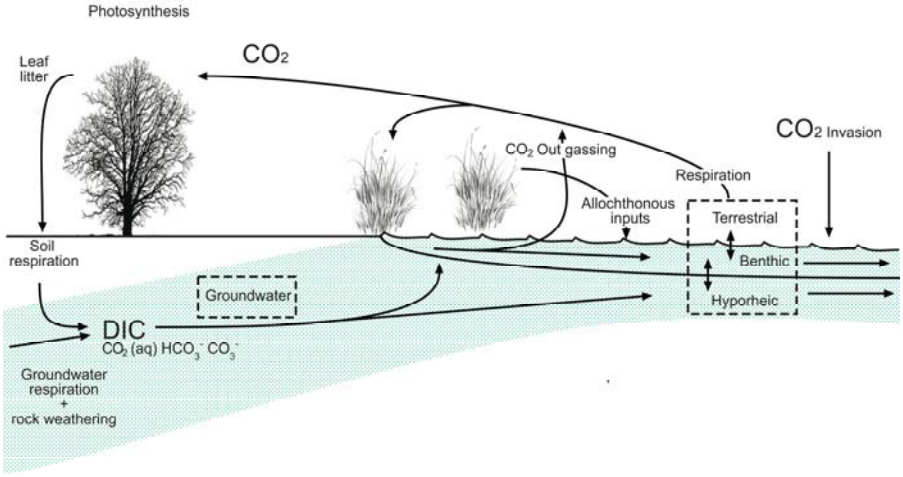

Figure 1. Conceptual diagram of the major pathways, forms and isotopic values of carbon that influence autochthonous spring ecotones in a braided river floodplain. Dashed boxes are food-webs (see Figure 2).

Lateral, vertical and longitudinal hydrological linkages, coupled with temporal dynamism are defining features of braided rivers. Braided rivers typically have extensive flood plains which are hydrologically connected to the river and wider catchment (Brunke & Gonser 1997; Ward et al. 1999; Woessner 2000), and contain a diverse array of habitats

in a state of continual successional flux due to re-working of alluvium by floods (Arscott et al. 2000; van der Nat et al. 2003). Consequently, a complex 3-dimensional mosaic of heterogeneous aquatic and terrestrial habitats along the river and across the floodplain exists. In addition to hydrological connectivity which mediates material flux, there are numerous ecotones/boundaries between habitat "compartments", which are more or less porous to biotic interactions (Paetzold et al. 2005; Greenwood & McIntosh 2008). The potential material and individual based fluxes of carbon occurring between surface stream, hyporheic and riparian zone food-webs are outlined in Figure 2. Individual based carbon exchanges take the form of predation across a boundary, whereas material exchanges are the movement of resources to and subsequent consumption in an adjacent zone. Figure 2 also outlines the major pathways by which carbon from the atmosphere is incorporated into stream ecosystems i.e. as organic debris derived directly from riparian vegetation or as dissolved inorganic carbon in groundwater.

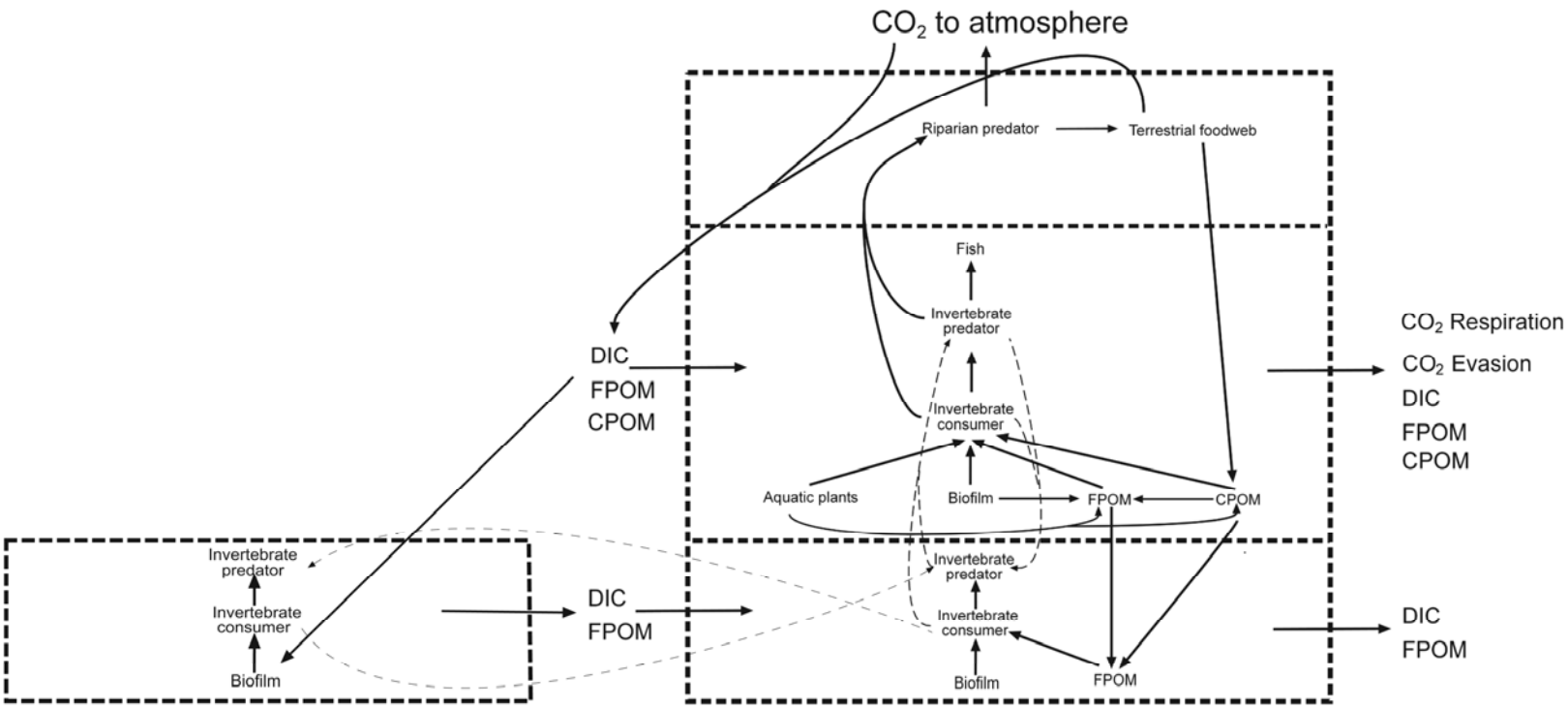

Figure 2. Schematic of potential food-web interactions and carbon fluxes between hyporheic, benthic and riparian zones of a stream. Dashed connection lines represent potential organism interactions between groundwater, hyporheic and benthic food-webs. Microbial pathways have been omitted for the sake of brevity.

Objectives

In this chapter I investigate the relative importance of the groundwater carbon pathway to the invertebrate communities of two spring streams. The compilation of organic matter budgets and comparison of gross primary production to total ecosystem respiration (P/R) has indicated that the ability of a stream to use inorganic carbon is dictated by the degree of riparian shading (Naiman 1982; Webster & Meyer 1997; McTammany et al. 2003). Therefore, I compared diversity and community structure in streams with riparian vegetation at different successional stages, i.e. forest and grassland. In chapter 4 I found no evidence of organismal linkages between stream and terrestrial food-webs in the form of predation by riparian spiders. Here I investigate the potential for reciprocal movement of energy between the spring stream and its hyporheic zone.

Methods

Study location

The Hawdon River is a 3rd order river on the east of the main divide of New Zealand's Southern Alps (Figure 3). The Hawdon catchment may experience torrential rain at any time of year associated with orographic rainfall in the Alps (Burrows 1977a). The friable nature of greywacke bedrock and high stream discharge result in an extensive alluvial floodplain which lies at approximately 600m a.s.l. The floodplain habitats in the Hawdon River exhibit a successional gradient which reflects magnitude of, or time since, flood disturbance. Areas of the floodplain that are regularly re-worked by river erosion consist of raw gravels, punctuated by islands of more stable surface material. Adjacent to the active river channels the floodplain surfaces are more mature, grading through bryophytes and lichens, tussock grassland and eventually to mature Southern Beech forest (*Nothofagus* spp) (Burrows 1977b; Reinfelds & Nanson 1993). The floodplain of the Hawdon valley also contains numerous spring-fed streams that up-well within palaeochannels (Stanford & Ward 1988) and derive flow from the alluvial aquifer. A substantial network of spring streams exists in both the forest and grassland floodplain areas (Figure 3).

Study design

Two adjacent spring streams were selected, one surrounded by forest and the other entirely within grassland. The floodplain forest and grassland areas in this study were estimated to be 100 – 350 and 40 - 100 years old, respectively (Reinfelds & Nanson 1993). Both springs had permanent flow (authors pers. obs. 2006-2009) and were of similar discharge and location within the upwelling complex (Figure 3). My previous assessments of $\delta^{13}C$ of DIC and food-web gradients in spring streams (Chapter 4) revealed rapid shifts in $\delta^{13}C$ over the first 10s of meters from the point of upwelling. Therefore, I chose to arrange sites along both streams on a log base 6 scale; 0, 6, 12, 24, 48, 96 and 192m from the source. I sampled the benthic and hyporheic zones of both streams. The hyporheic zone was sampled using standpipes inserted to a depth of at least 25cm and a self-priming bilge pump. Stand pipes were also inserted into the groundwater at -3m and -6m "upstream" of the spring source.

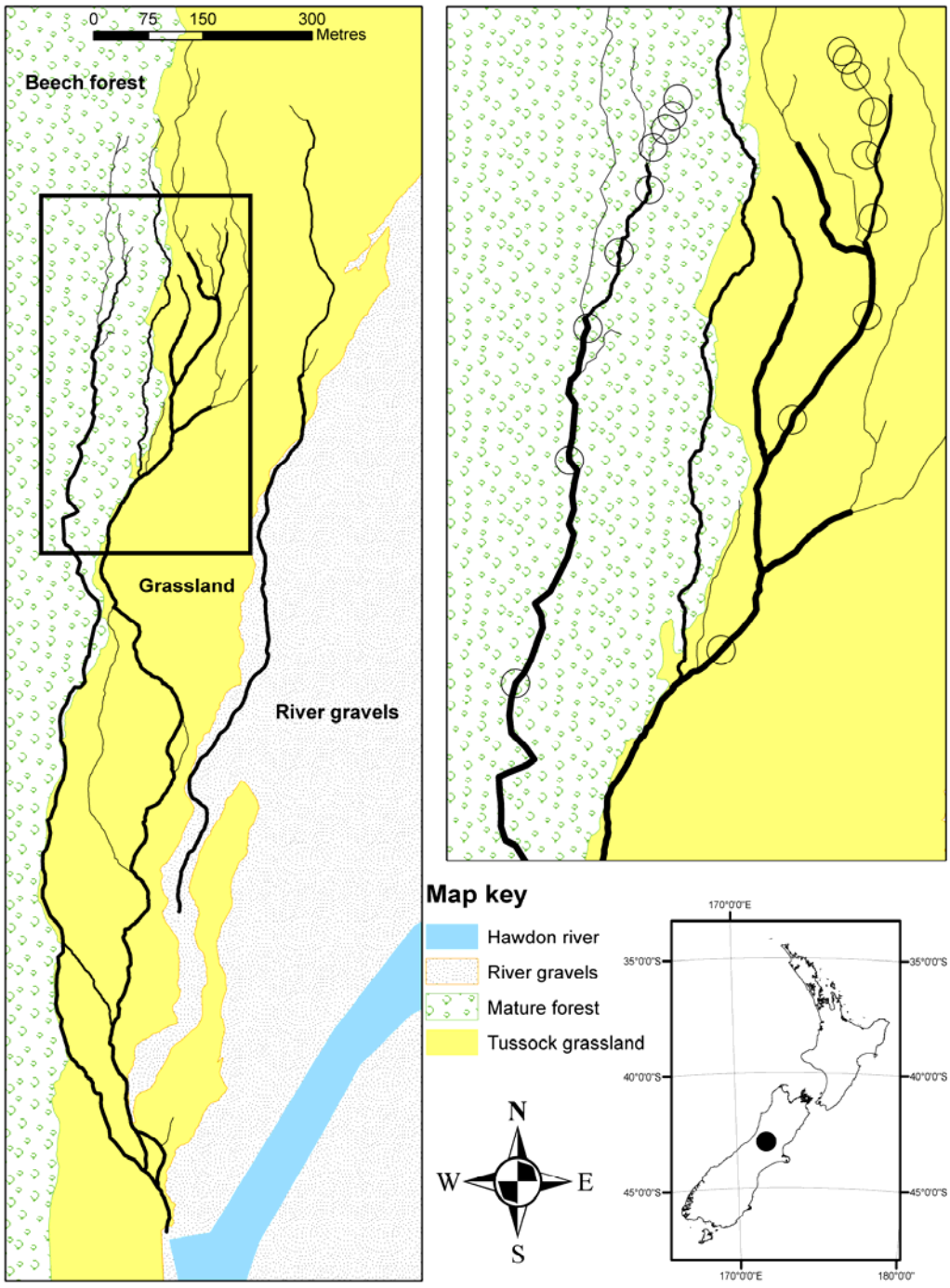

Figure 3. The network of spring streams within the floodplain of the Hawdon River, Canterbury, New Zealand. Vegetation cover of the floodplain is shown along with the location of longitudinally arranged benthic and hyporheic sampling sites (upper right inset) in forested and grassland spring streams sampled in June 2009.

Sample collection

Water chemistry

Samples for dissolved inorganic carbon (DIC) were collected in vacuum sealed 12 ml Exetainers which were opened beneath the surface of the water. Upon filling, the lid was replaced and the vial checked for gas bubbles. Water for dissolved organic carbon (DOC) analysis was collected in sterile 60ml containers. All samples were kept on ice until treatment with 0.01% sodium azide and shipping to the University of California Davis Stable Isotope Laboratory for analysis. Details of the specific analytical techniques are available at http://stableisotopefacility.ucdavis.edu/, (accessed July 2009). At each site temperature and conductivity (at 25^{o}C) were measured with a calibrated Oakton 10 conductivity/temperature meter. Dissolved oxygen was measured with a YSI 550 DO meter and pH with a Solstat FET pH meter that was re-calibrated before each measurement. Water and water chemistry samples of ground and hyporheic water were taken from the pump sampling receptacle during continuous pumping after all quantitative water sampling (for invertebrates and sediment) had been completed.

Stream community

At each benthic site quantitative biological samples were collected. These included three Surber samples (0.11 m^2, mesh size = 250 μm). All material within the samples was retained. Fine particulate organic matter (FPOM) was collected by placing a plankton net (mesh size = 53 μm) over the Surber sampler. Further samples of aquatic bryophyte, macrophyte, filamentous algae and FPOM for isotopic analysis were collected from mid-stream to reduce the likelihood that plants had been exposed to the atmosphere during periods of low flow. Biofilm was removed from at least four randomly selected stones using a tooth brush. All invertebrate or plant matter was removed from these stones prior to scrubbing. For isotope analysis additional aquatic invertebrates were collected from the stream by kick netting and handpicking. Quantitative groundwater and hyporheic invertebrate and FPOM samples were taken by pumping 20 litres of water through both a 250 μm mesh kicknet and 53 μm mesh plankton net. In order to enhance the collection of groundwater invertebrates a novel technique analogous to electro-bugging was used (Taylor et al. 2001). Briefly, a copper rod was driven into the substrate within 2 m of the

standpipe and an adapted Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, N.Z.) with 300–600 V pulsed DC (pulse width ~ 3 ms, 60 pulses s^{-1}) was used to send a current through the groundwater. This procedure increased the abundance of invertebrates collected in pump samples, presumably by dislodging individuals otherwise able to resist the flow created by pumping (author's unpublished data). Finally, allochthonous materials were collected in and adjacent to both streams. All material destined for isotopic analysis was returned to the lab and frozen, other samples were preserved in 70% ethanol. Benthic invertebrates were sorted, identified and enumerated under at 40X magnification. Identifications were made to the lowest taxonomic level possible (mostly genus), except for Oligochaeta, which were not differentiated below order, and Chironomidae, which were not separated below sub-family. Samples were dried for biomass estimations at 45^{o}C for at least 48 hrs before ashing at 500^{o}C for 4 hours.

Sample preparation and analytical techniques

Aquatic invertebrates, FPOM, bryophyte, macrophyte, filamentous algae, biofilm layer and allochthonous material samples were defrosted and checked at 40X magnification. All contaminant material was removed. Where possible aquatic invertebrates were eviscerated prior to drying. Gastropod shells were removed by manualy. All material was then dried at 45^{o}C for a minimum of 48 hrs before grinding. Ground samples were frozen at -80^{o}C prior to isotope analysis. Organic isotope analysis was performed at the Cornell Isotope Laboratory (COIL: http://www.cobsil.com/). Analyses were performed on a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyser. The overall standard deviation for the internal BCBG (plant) standard was 0.10‰ for δ^{13}C, the internal MINK (animal) standard was 0.08‰ for δ^{13}C, and the internal GNPS (soil) standard was 0.06‰ for δ^{13}C. Values were also corrected for linearity across amplitude gradients, the associated error of which was 0.35‰ for δ^{13}C.

Coarse particulate organic matter (CPOM) from Surber samples was separated into autochthonous and allochthonous components before drying and ashing at 500^{o}C for 4

hrs. All FPOM samples not intended for isotope analysis were also dried and ashed at 500^{o}C for 4 hrs. Separate hyporheic samples for isotope analysis were not collected so quantitative samples were sub-divided.

Estimations and statistical analyses

The partial pressure of carbon dioxide (PCO_2) in water samples was estimated using the relationship given by Doctor et al. (2008):

$$\frac{C_T \alpha_0}{K_H} = PCO_2 \quad (1)$$

where C_T is the total DIC concentration (mol C l^{-1}) in the sample, α_0 is the ionization fraction between CO_2 and H_2CO_3 (Stumm & Morgan 1981) and K_H is the Henry's law equilibrium constant for CO_2 in water. Because K_H is temperature dependent, its value was estimated from the temperature of the stream at the time of sample collection using the relationships provided in Telmer & Veizer (1999). Note however, that the values of K_1, K_2 (used to estimate α_0) and K_H should actually be pK (raised to the log base 10) to provide parts per million by volume (ppmV) values for PCO_2. Excess PCO_2 ($ePCO_2$) is the ratio of the calculated value of PCO_2 in the sample to that of the atmosphere which was assumed to be 387 ppmV. The $ePCO_2$ value is a multiplicative factor of the atmospheric concentration such that an $ePCO_2$ value of 10 is 10 times greater than the atmospheric concentration (Doctor et al. 2008).

All analyses of longitudinal change were performed using regression in the software package R, Version 2.5.1. Distance was log transformed for all analyses. Richness, density and biomass were represented by the mean value from three Surbers. Multi-dimensional scaling (MDS) ordination used log +1 transformed mean abundance data and the Bray-Curtis distance measure and was performed in PRIMER 5. Overall and pair-wise ß diversity was calculated using Whittaker's (1972) formula:

ß = total diversity / average diversity-1

Whittaker's ß diversity is a measure of the turnover of taxa between two or more sites. Values range from 0 to 2, with 0 representing identical diversity within sites and 2 representing total dissimilarity. Pair-wise Whittaker's ß diversity was calculated and Mantel tests (using 10,000 permutations) were performed using the r program "betadiver" in the package vegan (r core users group 2009). The nestedness metric was calculated using the software package BINMATNEST (Rodríguez-Gironés & Santamaría 2006)

Results

Stream physico-chemistry

Discharge in both forest and grassland spring streams was similar for the first 48m after which the forest spring stream increased relative to the grassland stream to approximately three times the discharge at 192m, 2.9 $m^3 s^{-1}$ and 0.8 $m^3 s^{-1}$ respectively. This resulted from merging with an adjacent spring-fed tributary and numerous seepages. Generally water chemistry parameters in the grassland stream changed markedly downstream (Table 1). pH, dissolved oxygen saturation, $\delta^{13}C$ DIC and $\delta^{13}C$ DOC increased whereas conductivity, $ePCO_2$ and DOC declined downstream. In contrast, water chemistry of the forest stream showed no significant change downstream, except $\delta^{13}C$ DOC, which increased. The range in pH, dissolved oxygen saturation and conductivity were comparable in both streams. However, the forest stream was consistently colder than the grassland stream and $\delta^{13}C$ DIC at the source of the forest spring was almost 2‰ more enriched than in the grassland spring, despite a similar range of $ePCO_2$ values in both streams.

Table 1 Physico-chemical variables measured in the forest and grassland spring streams, source and downstream values. *P* values in bold indicate a significant relationship with distance. $\delta^{13}C$ DIC, $ePCO_2$, $\delta^{13}C$ DOC and DOC ppm data are means of three replicates; all other data are single measurements.

	Forest			Grassland		
	source	192m	*p*	source	192m	*p*
pH	6.6	7.1	0.61	6.2	7.4	**0.021**
DO (%)	79	81	0.37	85	98	**0.001**
Conductivity ($\mu S_{25} cm^{-1}$)	60	59	0.78	61	58	**0.045**
Temperature (^oC)	6.8	7.7	0.50	7.9	7.8	0.590
$\delta^{13}C$ DIC (‰)	-9.1	-9.6	0.21	-11.1	-9.7	**0.008**
$ePCO_2$	9	4.3	0.25	12.4	1.9	**0.002**
$\delta^{13}C$ DOC (‰)	-29.3	-24.2	**0.008**	-23.5	-22.3	**0.003**
DOC (ppm)	0.6	0.9	0.054	5.6	1.1	**0.029**

Neither total, allochthonous or autochthonous CPOM in the forest spring stream showed a significant relationship with distance from the source. This was partly due to a large spike in autochthonous CPOM at 96 m (Figure 4). The first 12 m of the spring had similar quantities of allochthonous and autochthonous material, primarily *Nothofagus* leaves and wood, and bryophytes. Below 12 m CPOM was dominated by bryophytes.

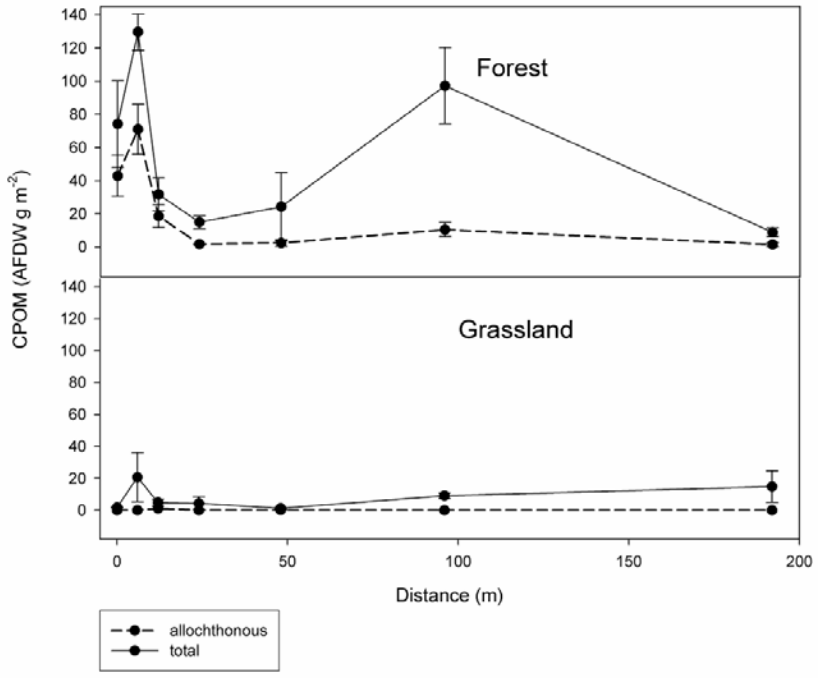

Figure 4. Benthic coarse particulate organic matter (total and allochthonous) along a longitudinal gradient of seven sites from the upwelling source to 192m downstream in a forest and grassland spring streams sampled in June 2009 (mean ± 1 S.E, n = 3).

The total quantity of CPOM in the grassland spring stream (mean 8 AFDM g m^{-2}) was markedly lower than in the forest spring stream (mean 54.4 AFDM g m^{-2}), although the majority of the grassland stream bed was covered by macrophytes. There was no significant downstream change in the amount of CPOM in the grassland stream. CPOM, which was almost entirely autochthonous, consisted of filamentous algae and *Callitriche stagnalis* at the upstream sites, but was dominated by *Myriophyllum* sp. downstream.

Benthic FPOM showed no significant longitudinal change downstream within or between the two spring streams, and demonstrated a marked longitudinal concordance between streams (Figure 5).

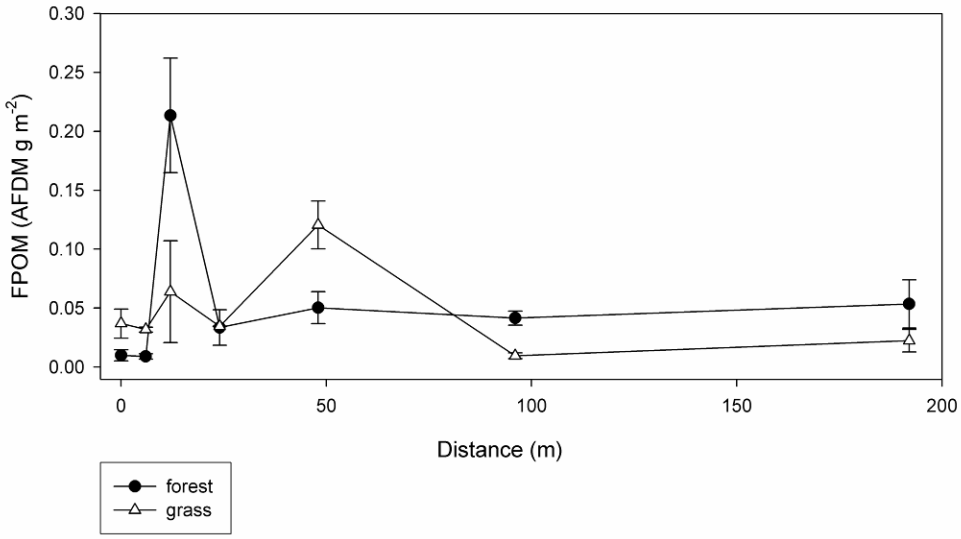

Figure 5. Benthic fine particulate organic matter along a longitudinal gradient of seven benthic sites from the up-welling source to 192m downstream in a forest and a grassland spring sampled in June 2009 (Mean ± 1 S.E. n= 3).

Benthic community composition

Fifty one taxa were identified from benthic samples; 32 in the grassland spring stream and 41 in the forest spring stream. Overall the five most abundant taxa were the gastropod *Potamopyrgus antipodarum* (46% of all individuals), the trichopteran *Pycnocentria* spp. (9%), a plecopteran *Spaniocerca zealandica* (8%), an ephemeropteran *Deleatidium* sp. and an amphipod *Paraleptamphopus* sp. (5% each). Ten taxa were found

only in the grassland stream, the most abundant of which were the predatory trichopteran *Hydrobiosis parumbripennis*, a gastropod *Austropeplea tomentosa* and a species of Diamesinae (Chironomidae). A further 19 taxa were found only in the forest stream, the most abundant being the plecopterans *Spaniocerca zealandica* and *Austroperla cyrene*, the ephemeropterans *Zephlebia* sp. and *Neozephlebia scita*, and the trichopterans *Baraeoptera roria* and *Olinga* sp. Of the taxa found in both streams the trichopterans *Oxyethira albiceps* and *Oeconesus* sp., a plecopteran *Zelandobius* sp. and the sandfly *Austrosimulium* sp. were most abundant in the grassland stream. Conversely, large individuals of *Chironomus zealandicus* were mostly encountered in the forest stream. The first 6 metres of the forest stream were numerically dominated by *Paraleptamphopus* sp. and *Spaniocerca zealandica*, whilst *Potamopyrgus antipodarum* was most abundant at the grassland spring source. In terms of biomass the forest spring source was dominated by *Spaniocerca zealandica,* the dipteran *Limonia* sp. and scirtid beetles, whilst the grassland spring source invertebrate biomass was dominated by gastropods and oligochaetes. Biomass in the lower reaches (sites 192 and 96) of both streams was dominated by gastropods and oligochaetes.

Mean benthic invertebrate richness in the forest spring stream increased downstream (r^2 adj. = 0.68, p = 0.014), however, richness in the grassland spring stream showed a significant hump shaped relationship with distance (r^2 adj. = 0.89, p = 0.005). However, it should be noted that in both streams there was considerable variation within the donwstream sites and so in fact richness may reach a plateau rather than decline or increase in the grassland and forest stream respectively (Figure 6). Neither density nor biomass showed a significant change downstream, however both showed a similar pattern in each stream (Figure 6).

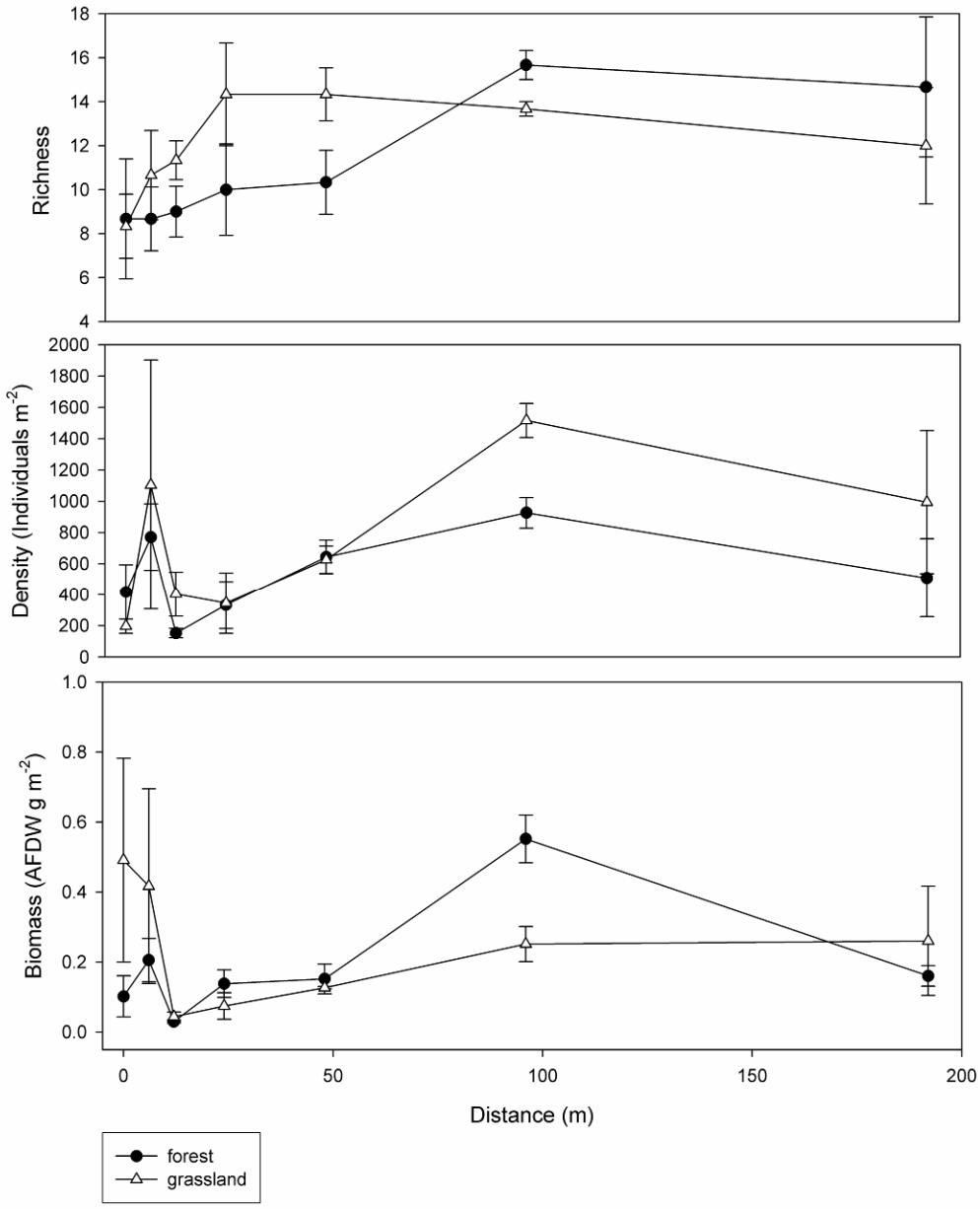

Figure 6. Benthic invertebrate richness, density and biomass along a longitudinal gradient of seven sites from the up-welling source to 192m downstream in a forest and grassland spring stream (mean ± 1 S.E, n =3).

An MDS ordination showed a distinct shift in the invertebrate community longitudinally with both spring sources clustered to the left of Axis 1 (Figure 7). The forest and grassland streams also had markedly different community assemblages.

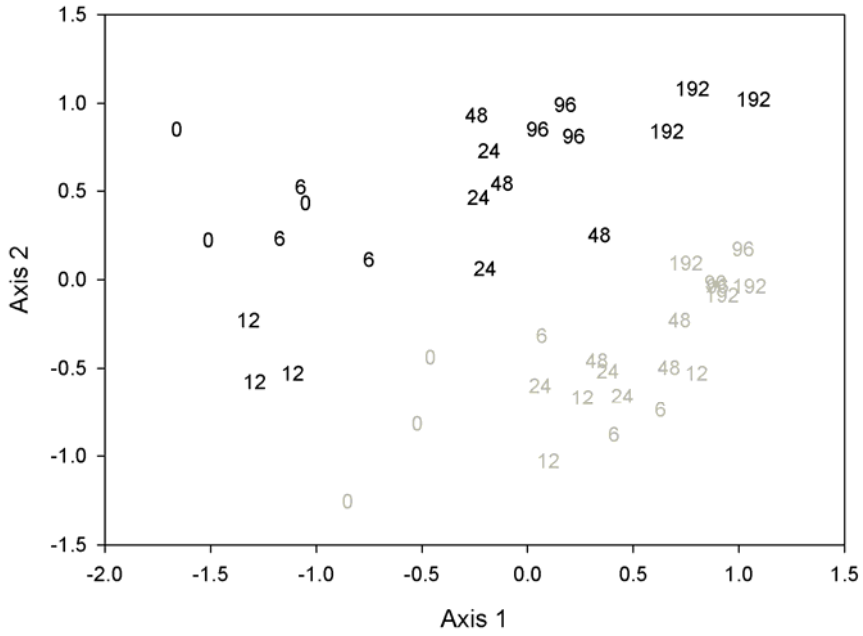

Figure 7. Multi-dimensional scaling (MDS) ordination of invertebrate communities based on abundance (log +1 transformed). Forest sites are shown in black, whilst grassland sites are gray. Numbers represent distance (m) from spring source. Stress = 0.19.

Overall Whittaker's ß diversity, or the turnover of taxa between all sites, was greater in the forest spring stream (1.5), compared to the grassland spring stream (0.7). Comparison of pair-wise Whittaker's ß diversity between sites within each stream showed that in both streams ß diversity increased with distance between sites and the pattern was much stronger in the grassland stream (Figure 8). However, the levels of pair-wise ß diversity were higher overall in the forest stream than in the grassland stream reflecting the turnover of a greater number of taxa.

An analysis of nestedness revealed that invertebrate assemblages at sites on the grassland spring stream were not significantly nested ($p = 0.106$) whereas those in the forest spring stream were ($p = 0.042$). Thus, in the grassland stream, it seems that source and downstream sites contained different taxa to the high diversity middle reach sites. The strong relationship between pair-wise ß diversity and distance downstream indicates there was a downstream pattern of species replacement; taxa were lost and new taxa were gained. In contrast, in the forest stream, taxa were accumulated downstream with

relatively little loss or replacement; low diversity source sites were a subset of the taxa found at the high diversity downstream sites. Consequently, the downstream turnover of taxa, and the relationship between pair-wise ß and distance was less pronounced; taxa were added, not replaced. The relative paucity of species replacements along the forest stream initially appears to contradict the greater dispersion of forested sites in ordination space (Figure 7). However, in the ordination greater overall richness at forested sites eclipsed the pronounced turnover of a lesser number of taxa in the grassland stream.

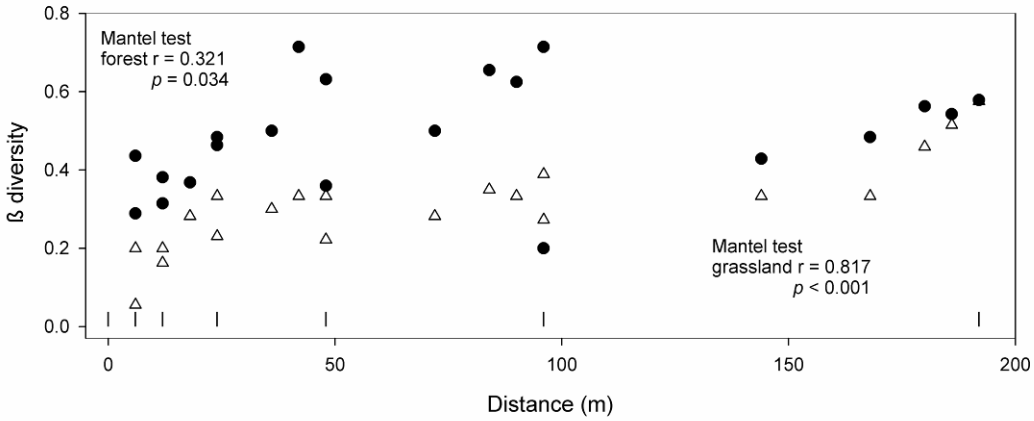

Figure 8. The relationship between ß diversity (taxonomic turnover between sampling sites) for each pair of sites and distance downstream. Grassland sites are open triangles and forest sites are closed circles. Sampling locations are shown by a vertical dash. Results of Mantel tests after 10,000 permutations are shown on the plot.

Isotopic variation of spring food-webs

The average $\delta^{13}C$ value of allochthonous materials collected within and adjacent to each stream was -28.5‰ (± 1 S.E. 0.34, n = 12), for the forest spring stream and -29.2‰ (± 1 S.E. 0.49, n = 8), for the grassland spring stream. These mean values for allochthonous material were used as a baseline from which to asses the influence of groundwater-derived carbon. Considerable variation in the $\delta^{13}C$ of putative basal resources was found in the forest and grassland streams, but there were no significant longitudinal trends for individual resources (Figures 9 & 10). In the forest stream, close to the up-welling point, food sources had a range of $\delta^{13}C$ values, which spanned the mean value for allochthonous materials. However, all food sources from downstream sites fell entirely below this mean value. FPOM, filamentous algae, bryophyte and macrophyte $\delta^{13}C$ values were

consistently depleted relative to mean allochthonous values, whereas biofilm was more variable. In contrast, putative resources in the grassland stream spanned mean allochthonous values along the entire study reach. Filamentous algae and bryophytes were always depleted relative to allochthonous values, but macrophytes, biofilms and FPOM values varied about the mean throughout the study reach.

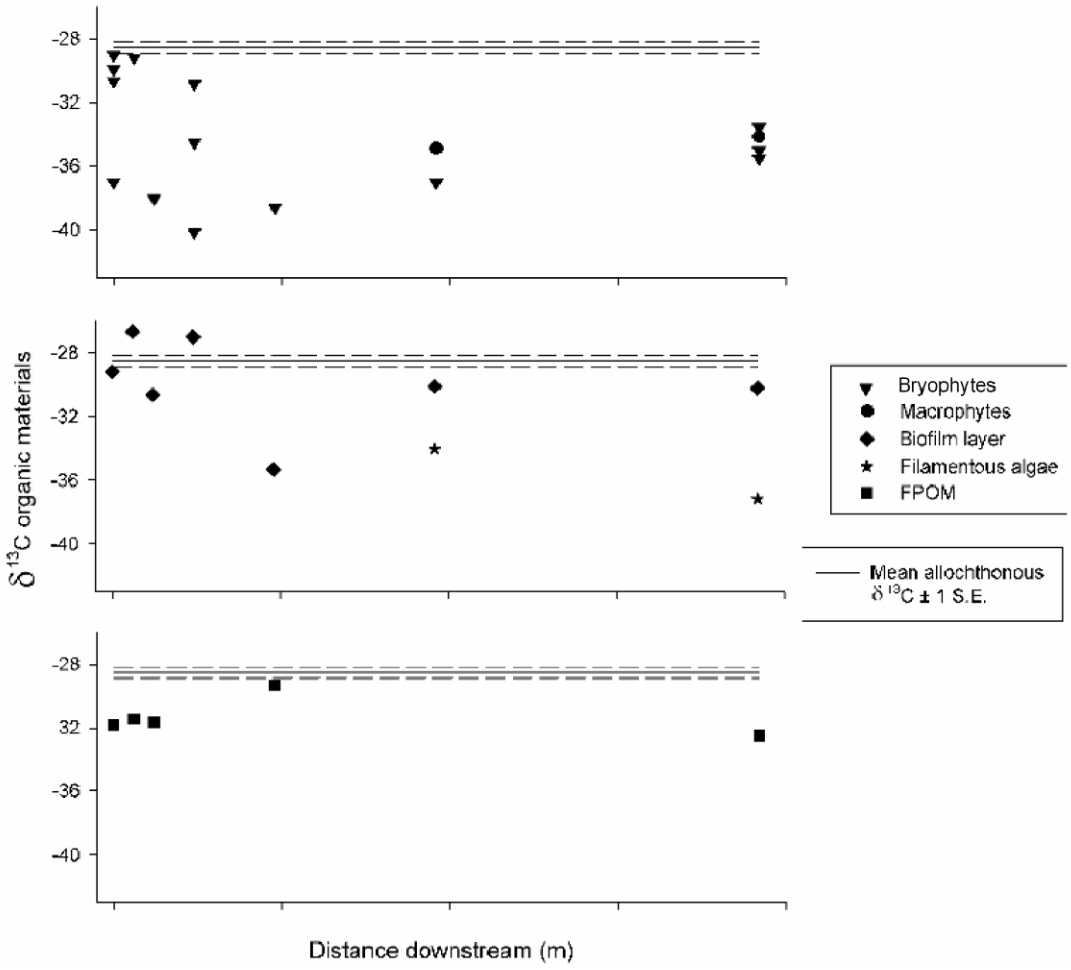

Figure 9. $\delta^{13}C$ of potential basal resources in the forest spring stream relative to a longitudinal gradient from the spring source and the average (± 1 S.E.) $\delta^{13}C$ of allochthonous materials collected adjacent to each stream.

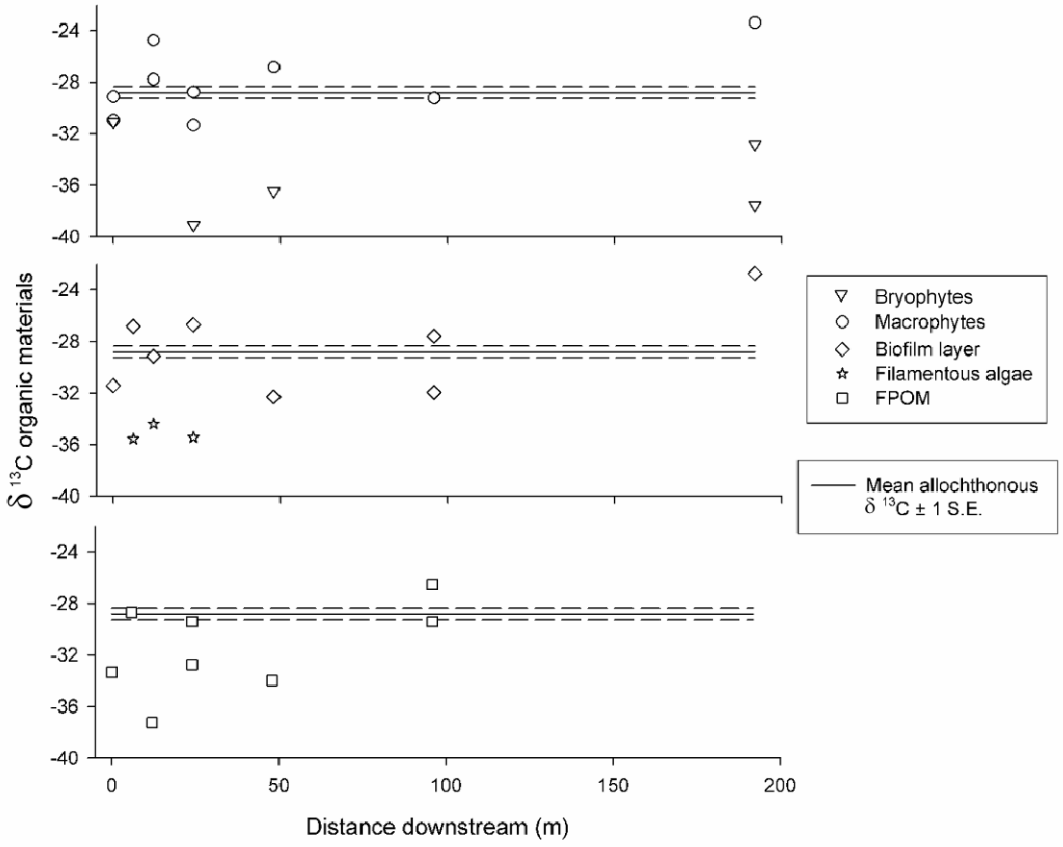

Figure 10. $\delta^{13}C$ of basal resources in the grassland spring stream relative to a longitudinal gradient from the spring source and the average (± 1 S.E.) $\delta^{13}C$ of allochthonous materials collected adjacent to each stream.

The $\delta^{13}C$ variation of invertebrate communities along forest and grassland spring streams suggests an important role for groundwater carbon in both (Figure 11). Taxa with a $\delta^{13}C$ value of less than –1 SE of the mean of $\delta^{13}C$ of allochthonous values are assumed to be partially or entirely dependent on groundwater derived (GWD) carbon. At the forest spring source invertebrate $\delta^{13}C$ values spanned allochthonous values, but become collectively more depleted downstream. In the grassland stream $\delta^{13}C$ show a "U" shaped response to distance downstream. Close to the source and at 192 m downstream the $\delta^{13}C$ values of invertebrates spanned allochthonous values, whereas in the middle reaches all taxa were relatively depleted in ^{13}C. In both streams taxa showing the most marked depletion (< -34‰) were *Limonia hudsoni*, *Pycnocentria* spp., *Zelandobius* spp., *Cura* sp.

and Hydrobiosidae. The latter two taxa are predators, whilst *L. hudsoni* is known to consume bryophytes. *Pycnocentria* spp. and *Zelandobius* spp. are collector-browsers which presumably feed on materials that represent a combination of materials of allochthonous and autochthonous origin.

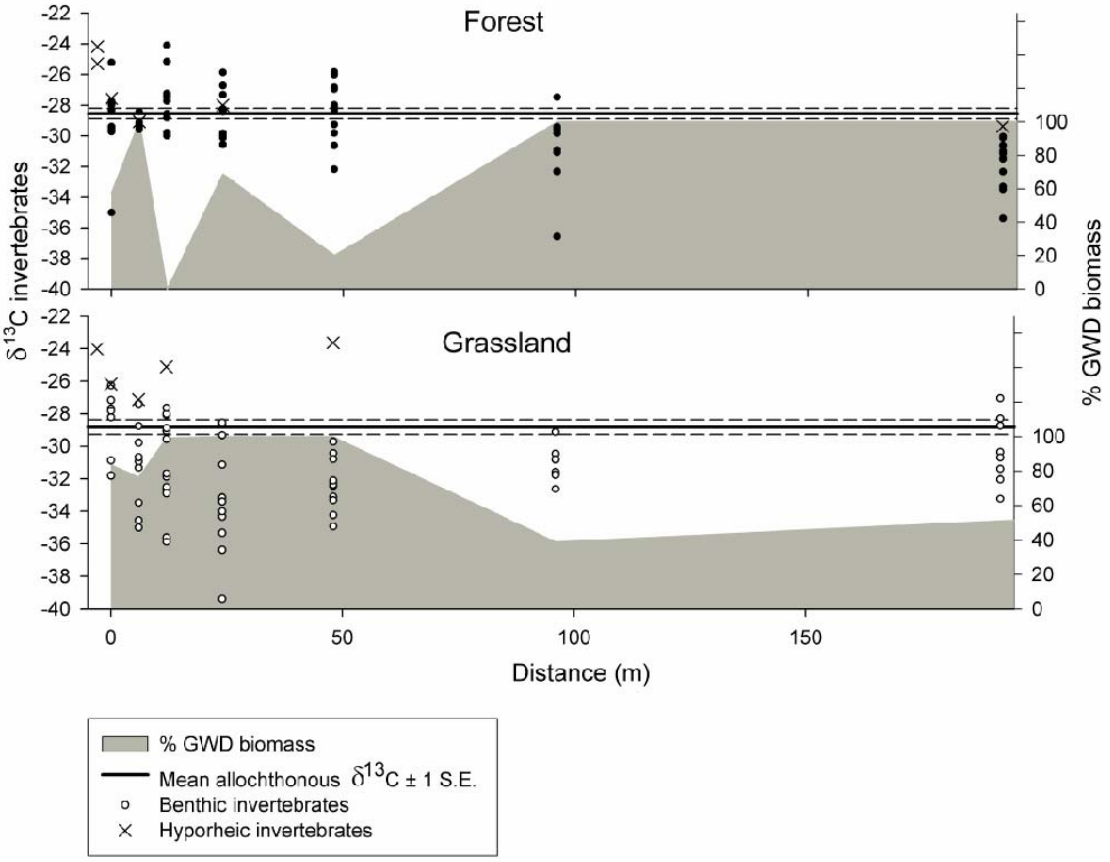

Figure 11. $\delta^{13}C$ of benthic and hyporheic invertebrates in a grassland and forest spring stream along a longitudinal gradient from the spring source and the average (± 1 S.E.) $\delta^{13}C$ of allochthonous materials collected adjacent to each stream. The percentage of total biomass represented by benthic taxa with a $\delta^{13}C$ of less than 1 S.E. of the mean allochthonous material $\delta^{13}C$ value is shown by the shaded area. These taxa are hypothesised to be partially or entirely dependent on groundwater derived (GWD) carbon.

In the grassland stream, at the source and downstream, both consumer and predatory taxa derived carbon from allochthonous sources. Larvae belonging to the collector-browser beetle family Scirtidae were consistently enriched relative to autochthonous values, but some other taxa had enriched $\delta^{13}C$ values in some reaches and depleted values at others. The biomass of GWD taxa (as a percentage of total community biomass) in the forest

stream was highly variable close to the source, but rose to 100% after 96 m. In contrast, community biomass at the source of the grassland spring was >80 % GWD, but declined after 48 m to approximately 50%.

Hyporheic taxa

The $\delta^{13}C$ of FPOM pumped from beneath both forest and grassland spring streams was highly variable, (forest, mean -29.9‰, range -42.2‰ to -22.3‰, grassland, mean -30.4‰, range -38.0‰ to -25.5‰) and showed no downstream trend. In total 17 taxa were found within the hyporheic and shallow groundwater zones of both streams; 198 individuals in 9 taxa in the forest stream and 141 individuals in 12 taxa in the grassland stream. Most common were the amphipods *Paraleptamphopus* sp. and *Paracrangonyx* sp. However, only six of the taxa found were represented by more than three individuals. Occasional hyporheos (*sensu* Gibert et al. 1994) included oligochaetes, *Deleatidium* sp., Tanypodinae and *Zelandobius* sp. Mean $\delta^{13}C$ of hyporheic invertebrates in the grassland stream showed no relationship with distance downstream, whereas forest stream invertebrates showed a significant negative relationship (adj. r^2 =0.49, d.f. 1, 5 p = 0.05) (Figure 11). $\delta^{13}C$ of hyporheic invertebrates in the grassland stream ranged from -23.6‰ to -27.1‰ and had a mean value of -25.3‰, compared to -20.2‰ to -29.4‰, mean -26.2 in the forest stream. These values suggest that hyporheic taxa predominantly use carbon derived from allochthonous inputs, biofilms and FPOM which incorporates allochthonous inputs or emergent macrophytes. The *Phreatoicus* sp. collected from beneath the 48m site of the grassland stream had a $\delta^{13}C$ of -23.6‰ suggesting it belonged to a separate food-web from the benthic taxa examined.

Discussion

Carbon pathways and community composition

Not surprisingly my results indicated that whilst the grassland spring stream system was primarily autochthonous, the forest spring stream used both allochthonous and autochthonous carbon pathways (Rounick et al. 1982). Allochthonous standing stocks in the grassland stream were low, although some benthic taxa, particularly at the spring source and 192 m site, had $\delta^{13}C$ values that were enriched relative to an allochthonous

signal. This may have been the result of either the use of atmospheric carbon by emergent aquatic plants, which were subsequently consumed by stream taxa, or the ingestion of terrestrial vegetation by taxa either in the stream or adjacent to it (e.g. scirtid beetle larvae). Conversely, both allochthonous (beech tree leaves and wood) and autochthonous (bryophyte) standing stocks at the source of the forest stream were high. Although bryophytes are largely inedible to the majority of benthic taxa found in these springs their decomposition contributes to CPOM, FPOM and the organic matrix which forms the biofilm layer (Suren & Winterbourn 1991; Winterbourn 2000). Consequently, the forest spring source contained a community that relied on both inorganic carbon from groundwater and allochthonous organic carbon from the riparian zone. However, with increasing distance downstream in the forest stream standing stocks of allochthonous material declined and as stream size increased, the allochthonous contribution was overwhelmed by autochthony. Both streams showed a steep size gradient; from seepage to large stream, with consequent shifts in community composition as also found by Barquin (2004). However, the forest stream also shifted its resource dependence downstream. Thus, a greater heterogeneity of niches might be available overall, and taxa were added, not replaced downstream as more niches become available. Conversely, in the grassland stream the carbon source (primarily inorganic carbon dissolved in groundwater) remained constant downstream. Thus, there might be fewer niches overall, and downstream changes were associated purely with increasing stream size. Potentially lower relative habitat/resource heterogeneity allowed source taxa to be excluded from downstream sites, thus creating non-nested, less diverse, longitudinal communities.

Subsidies across the vertical ecotone

Both groundwater derived inorganic carbon and allochthonous inputs of organic carbon represent cross-ecotone subsidies of fundamental importance to the recipient systems. However, my results also suggest a subsidy between the benthic and hyporheic zones, at least in the forested spring stream. Either groundwater invertebrates in the lowest reach of the forest stream used the benthic zone for feeding, or autochthonous benthic materials were transported into the hyporheic zone. The former alternative seems the less likely as groundwater taxa were not found in the benthos of the 192 m forest stream site and

FPOM from the hyporheic zone (average $\delta^{13}C$ value of -31.4‰, n = 3) was depleted relative to values for allochthonous materials. Although this result was limited to a single site (192 m in the forest stream) the incorporation of groundwater derived autochthonous carbon into the hyporheic zone in downstream reaches of spring streams seems likely. Thus, the initial subsidy of inorganic carbon from groundwater to the surface stream also drives a reciprocal energy feedback of organic carbon from the surface stream to the hyporheic.

The enriched $\delta^{13}C$ values found in groundwater and hyporheic taxa are likely to be produced via the same process driving $\delta^{13}C$ depletion of benthic taxa. Enriched (relative to allochthonous materials) $\delta^{13}C$ values arise from the breakdown of organic matter in soils (Dawson et al. 1995). Biochemical reactions and respiration in the soil discriminate against ^{13}C and result in relatively ^{12}C enriched values in the remaining organic matrix (Schweizer et al. 1999). However, these processes also produce ^{13}C depleted CO^2 which is incorporated into groundwater DIC. The highly enriched values found in some hyporheic taxa suggest they consume materials from biologically active soils, or biofilms within the aquifer.

Floodplain diversity

Spring-fed streams have been found to represent hotspots of biodiversity when compared to other braided river floodplain habitats (Chapter 2). In streams, disturbance, productivity and habitat heterogeneity are the factors most often associated with the regulation of diversity, but are notoriously difficult to disentangle (Death & Winterbourn 1995; Townsend et al. 1997; Vinson & Hawkins 1998; Field et al. 2009). Both the spring streams used in this study are at the most stable end of the disturbance gradient, and have been shown to have either high or intermediate levels of diversity depending upon context (Death & Winterbourn 1995; Townsend et al. 1997). Recent floods as a driver of stream invertebrate community structure can be excluded in the present study as both streams exhibited characteristics indicating the long term absence of disturbance. Historic disturbance of the floodplain can also be excluded as having a direct influence on invertebrate richness. The floodplain forest and grassland areas adjacent to the study

area were estimated to be 100–350 and 40-100 years old respectively (Reinfelds & Nanson 1993), however, the spatial proximity of reaches (approx. 100 m) and the existence of numerous other spring streams nearby suggest that dispersal of taxa should not limit richness in either system. The benthic invertebrate standing crop within these streams was high relative to adjacent run-off fed streams (Barquin & Death 2006), however there was no evidence of differences between the forest and grassland streams in terms of density or biomass. Therefore, whilst high standing crop contributes to the diversity of both streams in terms of overall productivity and species accumulation (Rosenzeig & Abransky 1993; Ugland et al. 2003) it cannot be invoked to explain differences between the stream communities. Rather the characteristics of the successional stage of riparian vegetation, indirectly regulated by time since disturbance, appeared to be most influential. The greater invertebrate richness of the forest stream may be the product of the availability of a multiple carbon sources and higher associated habitat heterogeneity/niche availability.

Floodplain invertebrate diversity encompasses communities in a range of water-bodies; disturbed main channels and side braids, stable ponds and spring streams. My results highlight the importance of the terrestrial floodplain as a source of dissolved inorganic carbon to spring-fed streams and suggest that the groundwater carbon pathway was dominant in both streams studied. Because the forest spring stream ecosystem was augmented by particulate allochthonous inputs it had a richer community and a different longitudinal diversity pattern from the grassland spring stream. Despite their differences both streams had high reach richness which contributes to high floodplain diversity that reflects the successional diversity of the stream riparian complex, interacting with groundwater upwelling.

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Chapter 6: Synopsis and Synthesis

Early ecological research on braided rivers focussed on the most obvious habitats; the main braids. Most of these studies characterised braided rivers as highly disturbed, species-depauperate, 'ecological deserts'. However, more recent work has taken a broader approach and recognised these systems and their floodplains as spatially complex, temporally dynamic habitats with high landscape- and reach-scale biodiversity (Ward et al. 1999).

Globally natural riverine systems are coming under increasing pressure from anthropogenic modification (Nilsson et al. 2005). Braided river floodplains in particular, are some of the most severely impacted natural systems on the planet, such that in most developed regions of the world few unmodified examples remain (Ward et al. 1999). As a result of this there has been growing awareness of the "opportunity cost" of river modification in terms of lost biodiversity and ecosystem services (Ward & Stanford 1995; Brunke 2002; Tockner & Stanford 2002; Hohensinner et al. 2004). New Zealand is fortunate in having numerous relatively un-impacted braided river systems, which occur across a range of climatic and topographic zones. Surprisingly, while New Zealand braided rivers have been the subject of significant geomorphological research (Reinfelds & Nanson 1993; Mosley 2001; Coulthard et al. 2007), there has been a relative paucity of studies on their ecology. At the end of chapter 1, I suggested several potential avenues of ecological research, the foremost of which was an assessment of large-scale ecological patterns in braided rivers. In terms of invertebrate communities this topic can be crudely condensed into the question, "are all braided rivers the same?"

Are all braided rivers the same?

This is a question of both applied and fundamental interest to resource managers and ecologists, and its answer is dependent upon the scale of observation. To address this issue I conducted a spatially nested, hierarchical survey of eleven braided rivers in the South and North islands of New Zealand focusing on benthic invertebrate diversity and community composition at multiple spatial scales. In each river, six reaches and up to

five floodplain habitats within each reach were sampled. From 203 sites I identified a total of 145 taxa. Benthic invertebrate diversity was highly variable at the island, river, reach and habitat-scales. At the local scale there was a common relationship between habitat type and invertebrate diversity. Over 70% of lateral floodplain habitats (i.e. spring sources, spring streams and ponds) had greater richness and 73% had greater abundance than their associated main channel. This diversity was most pronounced in spring streams which contain both groundwater and surface water taxa. Several mechanisms could provide explanations for this high diversity, in particular differences in physical and successional heterogeneity (Chapter 1 & 3), disturbance (Chapter 3), and carbon availability (Chapter 4 and 5). The high biodiversity of lateral habitats serves to highlight the need to consider the forces that regulate habitat heterogeneity within floodplains; flow regime, sediment input and anthropogenic impacts (Chapter 1). However, the predominant unit of river management is the catchment, and it is at this scale that it is important to identify patterns and uniqueness.

The abundance-distribution relationship is a universal law in ecology (McGill et al. 2007) and states that in any regional community we will observe a small number of ubiquitous (but highly abundant) taxa and many rare taxa with limited spatial distributions. Rare taxa, which may be represented by only a few individuals in tens of thousands collected, fit into two groups. Firstly, those that are rare because they have a limited spatial distribution, and are not encountered outside restricted biogeographic zones, secondly taxa that are widely distributed, but do not occur commonly in the habitat types considered. In terms of biodiversity and habitat uniqueness, it is the relative locations of the rare taxa in the system of interest that is important. Thus, are the rare taxa spatially clumped or distributed evenly across habitats? I investigated this question using the concept of beta diversity (Chapter 2). Total diversity (y) is a function of the number of taxa within a sub-unit (α) and the turnover of taxa between sub-units ($ß$). The multiplicative calculation of ß reveals the heterogeneity of taxa in space, but is less informative about their relative locations; high ß could occur between habitat A and B where A is highly speciose and B depauperate, although with some taxa shared, or when both A and B contain similar numbers of taxa, but those taxa are different. Alternatively,

the additive calculation of ß ($y = \alpha+ß$) essentially describes the greatest spatial scale at which taxa are unique, and hence integrates spatial turnover and the spatial clumping of taxa. I found, that a significantly larger than expected proportion of overall diversity occurred at the larger spatial scales suggesting that rare taxa are distributed fairly evenly across space, rather than being clumped within a set of sub-habitats. Thus, there is turnover of taxa between rivers, and in terms of rare invertebrates each river is unique. Such a pattern may be a universal property of rivers within a landscape, indeed of the distribution of life in any biological system, particularly at the large spatial scales considered here.

The ability of any taxon to persist within a particular habitat is a function of its ability to deal with the biological interactions and environmental conditions to which it is subjected. Although braided rivers are often viewed as physically dominated systems, there is a role for dispersal and biological interactions in shaping their communities. Disentangling the effects of biogeographic patterning from environmental determinism is pivotal to understanding the distribution of species. In Chapter 3 I addressed this question by using a multivariate technique to test the relative effects of space and environment on the invertebrate communities of braided rivers. Whilst the rivers considered within this study differed in terms of their physical characteristics, which were highly influential upon invertebrate communities, I identified spatial patterning accross habitats albeit collinear with environmental gradients. This result was due to biogeographic patterning (Boothroyd 2000) at large scales which affirmed the findings of chapter 2.

Connectivity

Connectivity or linkages, both physical and biological, between parts of a river(s) influence the structure of invertebrate communities within those rivers. Physical connectivity between a reach and its catchment regulates the habitat mosaic which forms a template for biological communities. Biological connectivity, such as dispersal (or lack of it), adds further complexity to community structure.

Vertical connectivity between surface and subsurface components of a braided river also occurs across a range of scales (Woessner 2000). It is mediated by water and ranges from the down-welling and subsequent up-welling of water, above and below a riffle, to the large scale patterns of wetting and drying seen in some intermittent rivers (Geist & Dauble 1998; Brunke et al. 2003; Larned et al. 2008). The low levels of physical disturbance found in streams derived from groundwater flow undoubtedly contribute to their attainment of high faunal diversity. However, the specific structure and function of stream communities is also greatly influenced by the nature of their carbon supply (Cummins 1974; Wallace et al. 1997). Organic carbon used as an energy source by stream fauna is commonly in the form of allochthonous inputs of terrestrial plant material, and/or aquatic plants supported by inorganic carbon dissolved in stream water. This inorganic carbon may be obtained from the atmosphere, be a by-product of in-stream respiration or contained within groundwater inputs (Allan & Castillo 2007). In Chapter 4, I showed that the biota of autochthonous spring streams use dissolved inorganic carbon derived from microbial respiration of terrestrial vegetation in soils and groundwater. At the spring source CO_2 was 2 – 7 times atmospheric pressure and the average $\delta^{13}C$ value of DIC was -12.7‰. However, 1.2 km downstream CO_2 was <1.5 times atmospheric pressure and the average $\delta^{13}C$ value of DIC was -9.6‰, in accordance with streams approaching chemical equilibrium with the atmosphere. The $\delta^{13}C$ of atmospheric carbon is approximately -8‰. Photosynthesis by terrestrial C_3 plants depletes this carbon to ~ -27‰ and this carbon subsequently becomes incorporated into soils. Soil respiration produces CO_2, with a similar isotopic signature to its parent material, which enters groundwater resulting in DIC with deplete $\delta^{13}C$ values and high partial pressures of CO_2 relative to the atmosphere. Upon discharge into surface streams this DIC is used by macrophytes and algae for photosynthesis or released to the atmosphere by out-gassing. Fractionation of carbon during aquatic photosynthesis results in further depletion in ^{13}C (reducing $\delta^{13}C$ by about 20‰) before carbon is incorporated into the invertebrate food-web. The aquatic communities of spring streams are therefore connected to the greater catchment by the cycling of carbon through floodplain components; terrestrial, subterranean and aquatic.

The habitat mosaic at any given point within a river is a product of the interacting effects of hydrology, sediment input and local valley morphology. Whilst being temporally dynamic, with high turnover of individual habitats, the proportions of habitat type remain relatively constant (Arscott et al. 2002; Latterell et al. 2006; Whited et al. 2007). The successional trajectory of a floodplain ranges from bare gravels to mature forest and in Chapter 5 I investigated the importance of successional development of riparian vegetation to the functioning of spring stream food-webs. Floodplain and catchment vegetation regulates energy and structure in spring streams via the soil-groundwater pathway, but also through direct allochthonous inputs of organic carbon to the surface stream. In the absence of significant allochthonous inputs the grassland spring stream invertebrate community was almost entirely dependent upon groundwater derived carbon. However, the forest spring stream community showed considerable reliance on direct allochthonous inputs at the source, but a shift to groundwater derived carbon downstream. Although biomass and density of invertebrates in each stream were similar, the forest stream contained a greater number of taxa overall and showed an increase in invertebrate richness downstream as compared to a hump shaped response in the grassland stream. These differences were best explained by the greater resource and habitat heterogeneity in the forest stream derived directly and indirectly from riparian vegetation; from allochthonous inputs and groundwater carbon. Overall, the floodplain stream invertebrate community was more diverse in the presence of a greater diversity of terrestrial vegetation types (i.e. both forested and grassland springs) interacting with groundwater up-welling.

Implications of my research

The results of my research provide a strong affirmation of the need for a holistic ecosystem view of riverine systems. Within a landscape perspective, rivers constitute dynamic local patches regulated by hierarchical environmental controls and connected through longitudinal, lateral and vertical linkages. Thus, a river is an interconnected, dynamic mosaic of aquatic and terrestrial floodplain elements, which provide the physical template for diverse biotic communities to occur and interact across a range of scales

(Poole 2002; Ward et al. 2002). The focus of this thesis was upon aspects of that interaction and showed that invertebrate communities of braided rivers are regulated by environmental factors (related to hydrology), biogeography and dispersal. The major pathways and cycles involved in the regulation of biological communities in braided river ecosystems are outlined in Figure 1. At the largest spatial scales climate and geology dictate the occurrence of braided rivers (Figure 1b). Biogeographic patterns and inter-catchment dispersal events then define the regional species pool. Within each catchment, discharge and sediment input interact with local valley morphology to create floodplain structure. Floodplain structure interacts with the geomorphological and biochemical sub-cycles within the diagram. The geomorphological cycle (top) encompasses the flux of water and materials, primarily sediment, through the active river bed and is the principle driver of the shifting habitat mosaic of the floodplain. The biochemical cycle (lower) involves the cycling of energy, nutrients and materials along the floodplain, between aquatic, terrestrial and subterranean compartments. The biochemical cycle feeds back to active channel geomorphology and floodplain structure, primarily via the role of vegetation in bank stabilisation and successional development. The specific structure of aquatic invertebrate communities is then the result of biogeography, dispersal, physical, chemical and biological cycling. Figure 1 could be made more complex by the addition of any number of further mechanistic links and structural components. For instance, floodplain stream communities influence the eco-systems around them, e.g. aquatic sources of nitrogen enhance the development of riparian vegetation (Milner et al. 2000), and stream insects provide food for riparian invertebrates (Paetzold et al. 2005; Greenwood & McIntosh 2008).

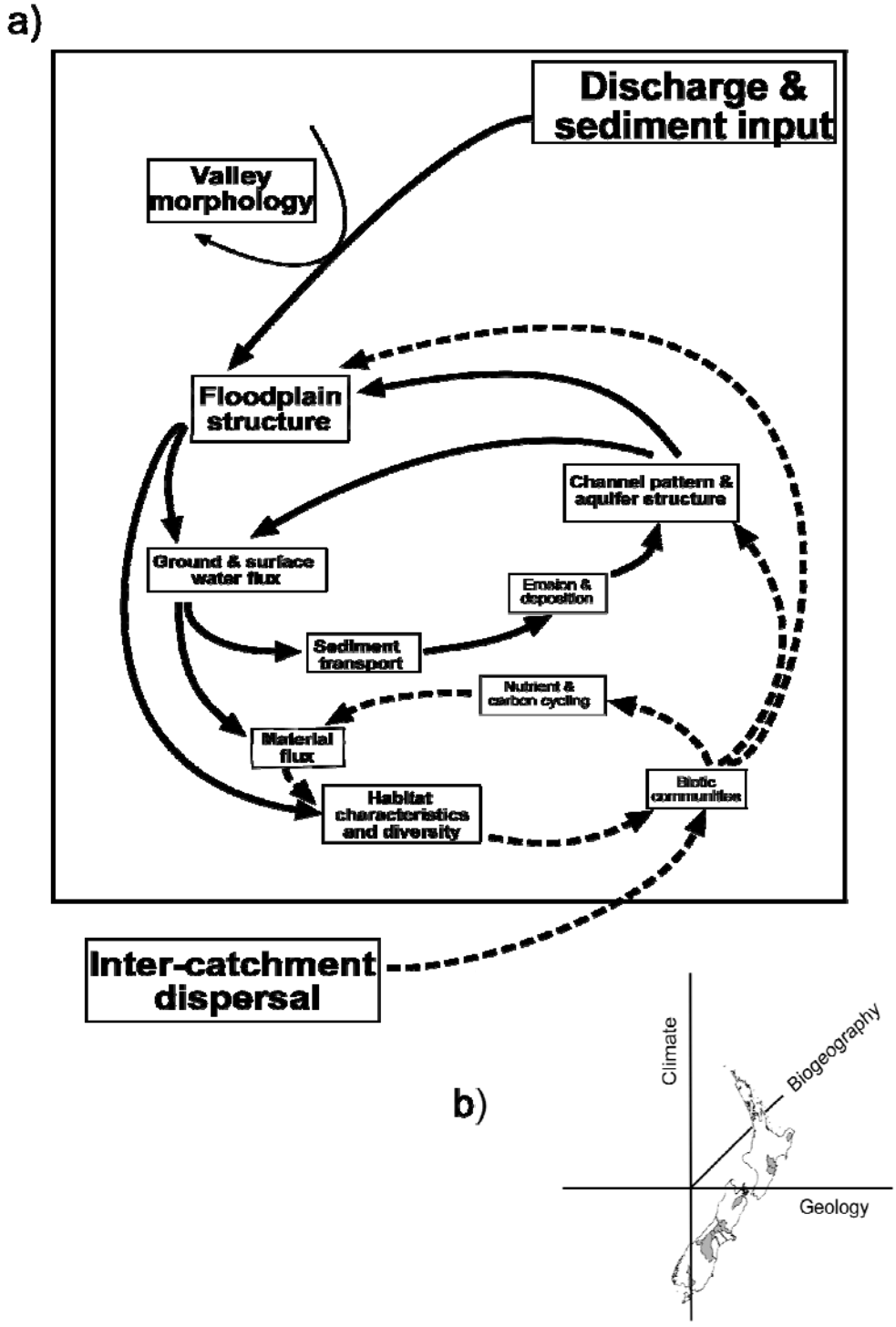

Figure 1. a) Conceptual diagram showing major fluvial landscape and biocomplexity dynamic pathways within a floodplain river catchment (large box) which enact upon biotic communities (adapted from Poole 2002). Text size represents spatio-temporal scale of processes. Solid lines represent physical linkages and dashed lines show chemical and biological linkages. b) Major spatio-temporal variables operating above the scale of catchments. The braided river catchments of rivers included in this study are superimposed.

In terms of resource management and conservation my findings have four major implications. First, the disproportionate contribution of broad spatial scales to overall diversity, suggests that a focus on the large-scale is most appropriate for the conservation of rare taxa. Overall diversity will be best protected by safeguarding whole catchments and protected catchments need to be replicated across broad scale gradients in hydrological regime and biogeography. Second, a general property of braided rivers is that greater taxonomic richness and invertebrate density occur in lateral habitats rather than main channels. The value of these lateral habitats cannot be overstated and they should be explicitly included within management plans. Thirdly, due to the spatial and hierarchical arrangement of diversity in braided rivers conservation managers need to ensure that assessments of biodiversity are made at the appropriate spatial scales. It is not sufficient to categorise the diversity of a river system based on the assessment of a single reach or main channel habitat. The spatial diversity of braided rivers requires lateral and longitudinally stratified sampling. Finally, each river exhibits a degree of dynamic stability, regulated by cross scale linkages and feedback (Figure 1). Any impact upon these linkages, such as climate change, land-use change, impoundment or channelisation will alter the nature of that dynamic balance. In order to predict the potential ramifications of any change we need a thorough understanding of the structure and function of braided river systems. I hope that the findings of this thesis have contributed to that understanding and may promote further research.

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Appendix 1

A new species of *Zelandobius* (Plecoptera: Gripopterygidae: Antarctoperlinae) from the upper Rangitata River, Canterbury, New Zealand

This manuscript has been published as Gray D.P. (2009) A new species of *Zelandobius* (Plecoptera: Gripopterygidae: Antarctoperlinae) from the upper Rangitata River, Canterbury, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **43**: 605-611. Published formatting has been retained.

Abstract

Zelandobius edensis n. sp. is described from a spring-fed creek in the headwaters of the Rangitata River catchment, South Canterbury, New Zealand. Adult males exhibit varying degrees of brachyptery and the only female collected also had short wings. Larvae are easily identified by their covering of long translucent hairs not found in other members of the *Zelandobius confusus*-group. The link between adult and nymph was confirmed by comparing 600-base-pair sequences of the mitochondrial gene, cytochrome c oxidase 1. Observations suggest the life cycle may be strongly synchronised by temperature constraints on nymphal growth and development, and/or a short season suitable for feeding and reproduction by the terrestrial adults.

Keywords stoneflies; brachyptery; taxonomy; alpine; SEM

Introduction

The stonefly genus *Zelandobius* Tillyard, 1921 is endemic to New Zealand and contains 29 described species in two species groups, the *Z. confusus* group (23 species) and the *Z. furcillatus* group (6 species) (McLellan 1993, 2008). Here a distinctive new species from material collected in a spring-fed tributary of the Frances River, Rangitata River system, Canterbury is described.

Materials and methods

All material was collected from a spring-fed tributary of the Frances River, Rangitata River catchment (NZMG 5757710N, 2328340E), South Canterbury, at 950 m altitude. Initial larval material was collected 22 April 2007, adults and further larvae were collected 18 May 2008. Both adult and larvae were collected by hand, in and adjacent to the stream. The holotype was a male and paratypes were 10 males, 1 female, and 5 nymphs. All material was stored in 100% ethanol. The description and measurements (to 0.01 mm) were performed using a 40× magnification dissecting microscope and 1 mm graticule. The link between adult and nymphal stages was confirmed by comparing the DNA from 5 individuals of each life stage. A 600-base-pair segment of the mitochondrial gene, cytochrome c oxidase 1 (COI) was sequenced. DNA was extracted from a tissue sample from the thorax or leg using the PureLink™ Genomic DNA Mini Kit (Invitrogen, New Zealand) according to the tissue extraction protocol supplied by the manufacturer. Polymerase chain reactions (PCR) were performed in 50 µl volumes with the reaction mixture containing 20 ng of DNA, 400 n*M* of each primer LC01490 and HC02198 (Folmer et al. 1994), 0.2 m*M* dNTPs (Roche Diagnostics, New Zealand), 1 × Taq PCR buffer (Invitrogen, New Zealand), 1 U Taq DNA polymerase (Invitrogen, New Zealand) and 1.5 m*M* MgCl2 (Invitrogen, New Zealand). The reaction mixture was held at 94°C for 2 min followed by 35 cycles at 94°C for 30 s, 45°C for 30 s, 72°C for 1 min, with a final extension at 72°C for 7 min. PCR reactions were run on an iCycler thermal cycler (Biorad, United States). PCR products were visualised on 1.5% agarose gel and then purified using a High Pure PCR product purification kit (Roche Diagnostics, New Zealand). Sequencing was undertaken using Big Dye v.3.1 on an ABI Prism 3100

Genetic Analyzer (Applied Biosystems). Sequences obtained in this study were deposited in the NCBI GenBank database under accession numbers FJ424816 – 25. The holotype was deposited in Canterbury Museum (CMNZ), Christchurch, New Zealand, and 2 paratype adult males and two nymphs were deposited in New Zealand arthropod collection (NZAC), Aukland.

Systematics

Family GRIPOPTERYGIDAE

Sub-family ANTARCTOPERLINAE

Genus *Zelandobius* Tillyard, 1921

Species *Zelandobius edensis* n. sp.

Material examined

Holotype Adult male from a spring-fed tributary of the Frances River, Rangitata River catchment (NZMG 5757710N, 2328340E), South Canterbury, at 950 m altitude. Deposited in Canterbury Museum (CMNZ).

Paratypes Ten males, 1 female and 5 nymphs collected from the same location. Same data as holotype. Two male adults and two nymphs deposited in New Zealand arthropod collection (NZAC).

Additional material Twenty-four nymphs from type locality.

Description Male body length 7.7–8.2 mm (mean 7.9 ± 1.1 mm SD), forewing length 4.0–8.5 mm (mean 6.7 ± 0.7 mm SD), head capsule width 1.4–1.7 mm (mean 1.5 ± 0.1 mm SD), antenna length 7.5–10.2 mm (mean 8.5 ± 4.2 mm SD), cercus 0.7–1.0 mm (mean 0.9 ± 0.3 mm SD). Female body length 9.0 mm, forewing 4.8 mm, head width 2.0 mm, antenna 6.0 mm, cercus 0.5 mm. Nymph (final instar): body length 11.5–12.0 mm; head width 1.8–1.9 mm; antenna 4.0–4.2 mm; cercus up to 2.0 mm (broken in most larvae).

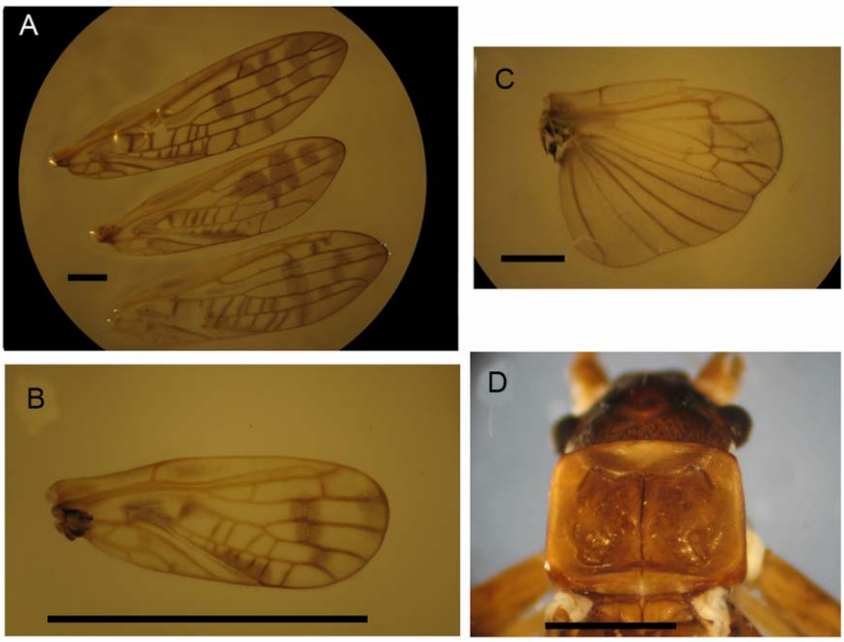

Fig. 1 A, Forewings of male *Zelandobius edensis* n. sp. showing variable lengths and patterning, scale bar = 1 mm. **B**, Short male forewing, scale bar = 4 mm. C, Short hindwing of male, scale bar = 1 mm. D, Pronotum of adult male, scale bar = 1 mm.

Adult Wings of variable length (4.0–8.0 mm, mean 6.7 ± 1.0 mm SD): fully-formed or showing various degrees of brachyptery (Fig. 1A–C). Short wings with fewer cross-veins and all wings may lack the posterior radial fork characteristic of most *Zelandobius* species. Forewings sub-hyaline and variably patterned with irregular, sometimes coalescing, grey patches surrounding distal cross-veins (Fig.1 A,B). Hindwings uniformly hyaline (Fig. 1C). General body colour dark brown; body with a coating of short pale hairs and some longer translucent hairs around pronotal margins and on ventral and lateral surface of thorax and pleurites. Antennae longer than body, of about 50 segments covered in short dark setae. Head with a coating of pale hairs, dark brown anteriorly with a variably distinct pale patch on the frontoclypeus. Epicranium lightly mottled. Ocelli difficult to see. Segment 5 of maxillary palp about twice the length of segment 4. Pronotum light-medium brown with variably dark mottling, but paler marginally and with a dark longitudinal groove in the mid-line (Fig. 1D); width: length ratio 1.2–1.5; all pronotal margins angled upwards slightly giving a flange-like appearance. Metanotum about 0.75 times width of mesonotum. Legs a uniform golden-

brown with a coating of short setae most obvious on the tibiae and tarsi; ventral margins of femora with parallel ridges bearing long translucent hairs. Abdomen of male chestnut-brown ventrally with parallel-sided pale patches laterally on each sternite. In the single female, the pale patches on sternites 2–7 were triangular and broader anteriorly. Abdominal tergites with a dark band posteriorly.

Male genitalia (Fig. 2–3) Medial sclerite of tenth tergite with strongly sclerotised margins; membranous cone with a short, narrow, parallel-sided neck and a coating of tiny black setae; posterior margin of tenth tergite produced as an almost spherical upturned knob, ventrally concave. Epiprocts with 5–7 pairs of marginal teeth, the basal tooth three times the size of the others; tip of basal tooth weakly bifid (Fig. 3D,E); epiproct tip slightly curved, parallel-sided and rounded terminally; ventral hook sharply pointed. Paraprocts narrowest basally, with a strong curved apical spine; upper margin with a shallow bulge below spine. Subgenital plate covered in pale hairs round its posterior margin. Cerci 9-segmented, curving ventrally.

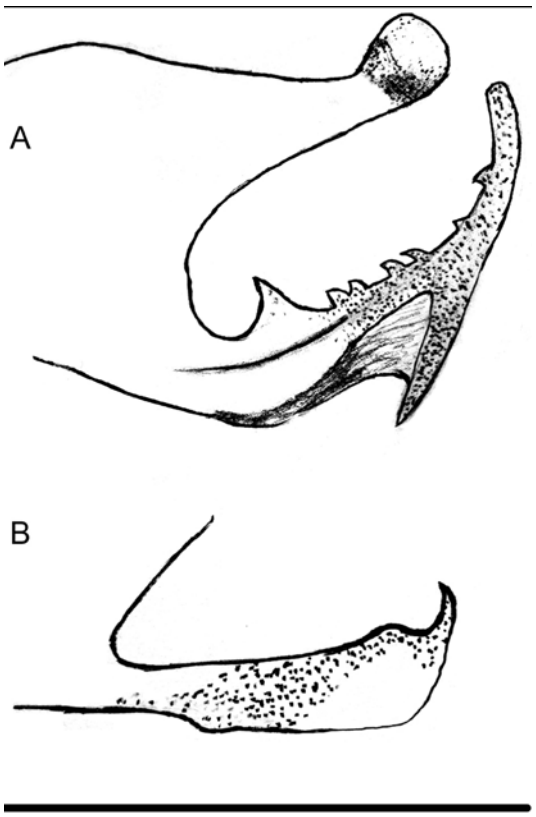

Fig. 2 Lateral view of: **A**, male tergite 10 and epiproct; **B**, male paraproct of *Zelandobius edensis* n. sp. Scale bar = 1 mm.

Female genitalia (Fig. 4) Subgenital plate (sternite 8) unicolorous with a pronounced rounded concavity on its posterior margin; this margin upturned in ventral view to form a ridge that extends over sternite 9. Sternite 9 membranous, extending slightly onto sternite 10. Sternite 10 fully sclerotised, its posterior margin and the subanal lobes with medium-length translucent hairs.

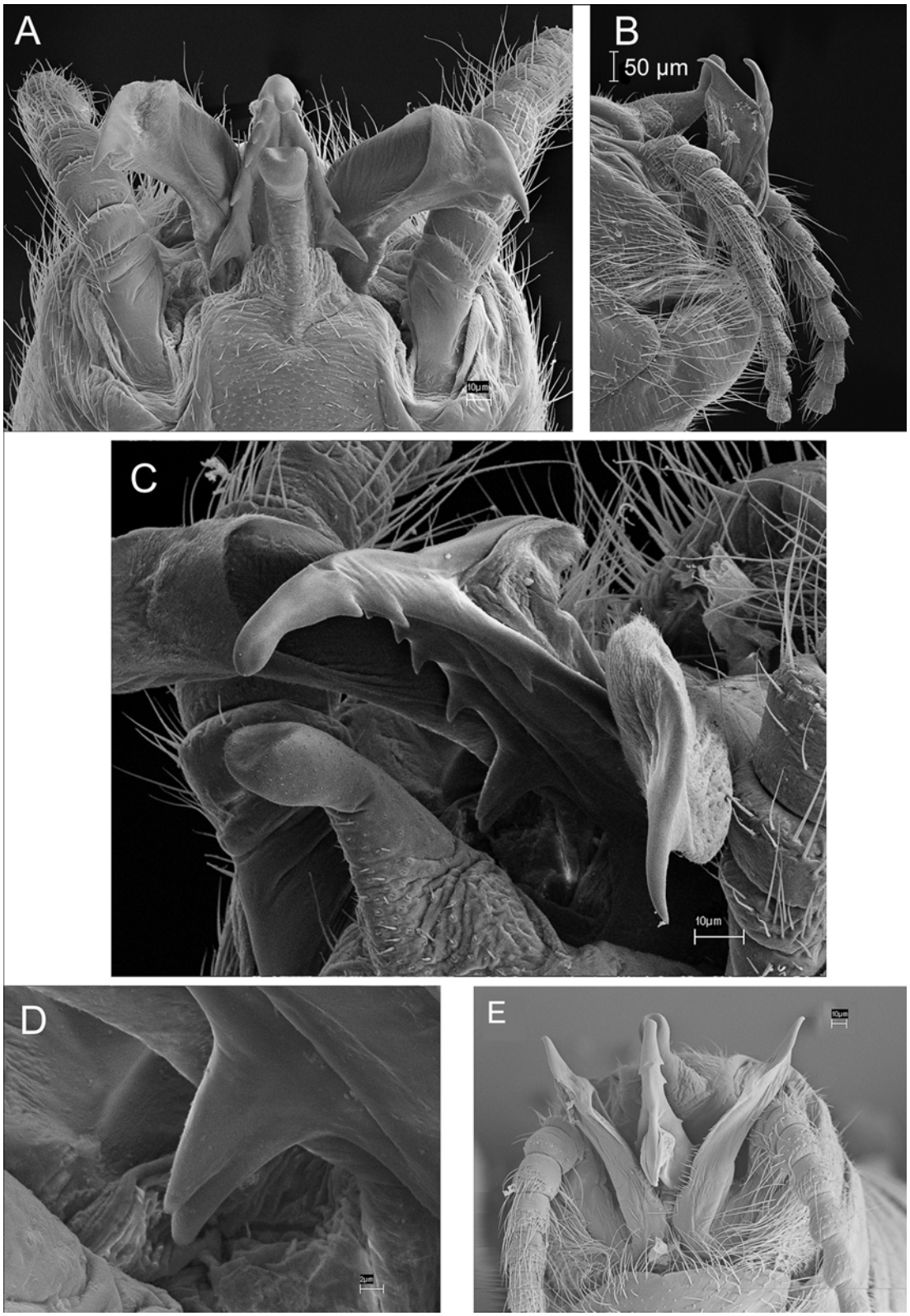

Fig. 3 Male genitalia of *Zelandobius edensis* n. sp.: **A**, dorsal view; **B**, lateral view; C, oblique view showing epiproct and tergite 10, note bifid basal tooth of epiproct; D, bifid basal tooth of epiproct; E, posterior view of male reproductive organs.

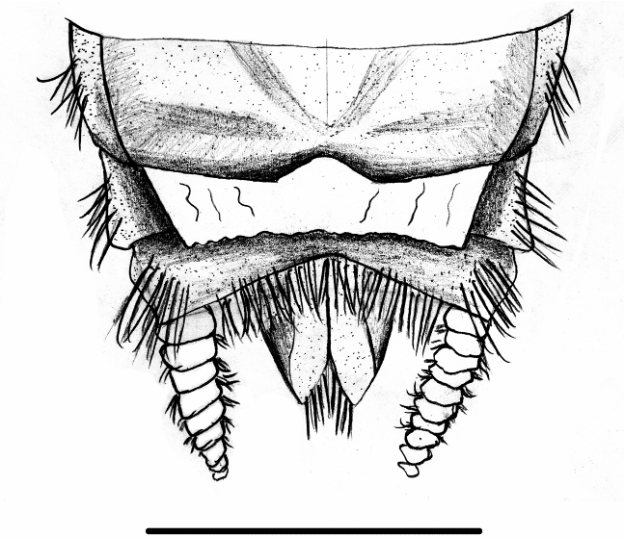

Fig. 4 Female genitalia of *Zelandobius edensis* n. sp., ventral view. Scale bar = 1 mm.

Nymph (Fig. 5a–c) General colour sandy brown/tan, the body including head and legs covered in translucent hairs up to about 0.25 mm long in the final instar. Epicranium lightly mottled in mid-instar larvae but plain in later instars. Scape of antenna bearing a few long translucent hairs, but these are absent from the pedicel and flagellum. Labrum hairy. Ocelli prominent. Pronotum rectangular with rounded angles and edges curved upward as in the adult; width: length ratio 1.4–1.6 in middle instars, 1.3–1.7 in late instars. Hairs cover the entire pronotum but are denser along the margins. Meso- and metanota covered in hair, their posterior margins re-entrant. Legs coated in hairs; tibiae and femora of equal length. Abdomen lacking a longitudinal dorsal ridge; each segment with a ring of darker pigmentation anteriorly and a fringe of dense, dark, medium length hairs posteriorly. Tergite 10 slightly longer than broad, straight sided with a distinct fringe of medium length dark hairs along its posterior margin. Cerci less than one quarter length of abdomen. Anal gills a well developed rosette. Subanal lobes tongue shaped. There was 98.7% similarity between 600-base-pair sequences of the COI gene providing conclusive evidence that both nymphs and adults were the same species.

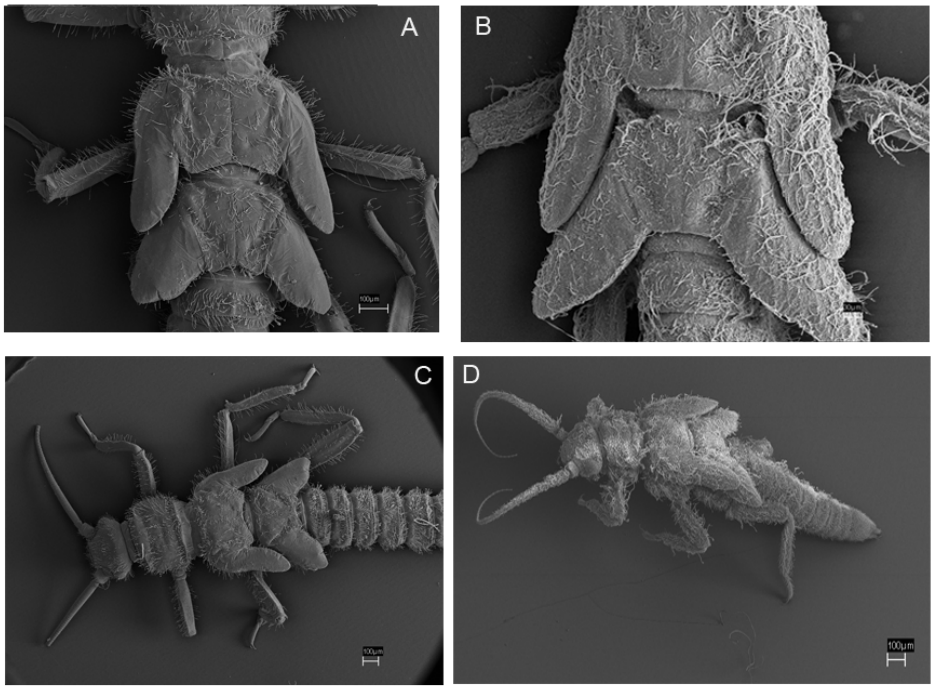

Fig. 5 A, Re-entrant hind margin of the meso- and metanotum of *Zelandobius edensis* n. sp. (*Z. confusus*-group); **B**, straight hind margins of *Z. pilosus* (*Z. furcillatus*-group); C, late instar larva of *Z. edensis* n. sp. without hairs on antennae; D, late instar larva of *Z. pilosus* with antennae covered in hairs.

Diagnosis Both nymph and adult of *Zelandobius edensis* n. sp. are readily distinguishable from other members of *Zelandobius*. *Zelandobius edensis* n. sp. is a typical member of the *Z. confusus*-species group, in that the distal cross-veins of the forewing are surrounded by dark, coalescing ovals of pigment, and the nymphal meso- and metanota have distinctly re-entrant hind margins (Fig. 5) (McLellan 1993). It can be distinguished from all other described species, by a combination of genitalic characters in the male and female and the well-developed hairiness of the nymphs. The form of the male epiproct of *Z. edensis* n. sp. differs from that of all other described species in having 5 or 6 pairs of small marginal teeth, a very large pair of proximal teeth, and a sharply pointed ventral hook. Similarly large proximal teeth are also found in *Z. confusus* Hare (1910), *Z. cordatus* McLellan (1993), and *Z. dugdalei* McLellan (1993), but not in combination with the other features mentioned above. The paraprocts of *Z. edensis* n. sp. are most similar to

those of *Z. patricki* McLellan (1993) as they possess a long curved apical spine and a shallowly bulged dorsal surface. However, the epiprocts of *Z. patricki* lack the very large proximal teeth found in *Z. edensis* n. sp., the ventral epiproct hook of *Z. patricki* is markedly blunter and the tip of tergite 10 is noticeably more bulbous in *Z. edensis* n. sp. than in *Z. patricki*. In the female, the combination of unicolorous subgenital plate (sternite 8), membranous sternite 9, and fully sclerotised sternite 10 distinguish *Z. edensis* from all other *Z. confusus*-group species.

The hairy nymph of *Z. edensis* n. sp. is most likely to be confused with that of *Z. pilosus* Death (1990), which also has its head, body and legs covered with long (c. 0.2 mm) translucent hairs. However, *Z. pilosus* belongs to the *Z. furcillatus*-group, and is distinguished by the straight rather than re-entrant hind margins of the meso- and metanota. Additionally, the antennae of *Z. pilosus* are hairy (Death 1990), whereas those of *Z. edensis* are not.

Etymology The specific name *edensis* refers to a large icefield, The Garden of Eden, which dominates the Frances River and forms its source. Eden is a Hebrew word meaning delight or pleasure.

Discussion

Zelandobius edensis n. sp. is known only from a single 30-m-long spring creek, which emerges from the base of a debris flow on Tauroa creek adjacent to the Frances River, a tributary of the Rangitata River. The creek is approximately 1.5 m wide, with a maximum depth of 30 cm, and lies at an altitude of 950 m a.s.l. about 4 km east of the main divide. Adults were found beneath stones alongside the creek, and nymphs in clusters on the undersides of cobbles and boulders in the water. Neither nymphs nor adults were found in association with the nearby Frances River. Alpine habitats are characteristic of *Z. confusus*-group species, with at least 13 of the other 21 described species being known only at altitudes greater than 900 m (McLellan 1993).

Middle-sized nymphs were collected on 22 April 2007, but neither adults nor larvae were seen on 25 August despite intensive searching. But on 18 May 2008, numerous late instar nymphs and adults were found at the site. These observations suggest the life cycle may be strongly synchronised. Seasonal synchrony has been postulated for various invertebrates that occupy high altitude habitats (Danks 2007; Hollmann & Miserendino 2008) and may be regulated by temperature constraints on nymphal growth and development, and/or a short season suitable for feeding and reproduction by the terrestrial adults.

Wing length of male *Z. edensis* collected in the alpine spring stream varied considerably and the single female found had short wings. Of the other 21 *Z. confusus*-group species, some degree of brachyptery has been found in the males of six species and the females of five species, one of which is wingless (McLellan 1993). However, males have not been described for five further species and females are unknown in three, so the incidence of wing length reduction in the species group as a whole may be greater than known at present. Both sexes of three alpine species, *Z. foxi* McLellan (1993), *Z. macburneyi* McLellan (1993) and *Z. montanus* McLellan (1993) exhibit some degree of brachyptery. In Plecoptera, reduced wing size and loss of flight have been associated with rarity: short-winged or wingless taxa are rarer than fully-winged species (Malmqvist 2000). In *Zelandobius*, constraints imposed by the alpine climate may have promoted wing size reduction, thereby contributing to the isolation of species like *Z. edensis* and their consequent rarity.

Lastly, females are more commonly flightless than males in insects in general, but the reverse has been found in stoneflies (Roff 1990). Flightless male insects are frequently associated with flightless but mobile females (Roff 1990). This mobility presumably compensates for any reduction in the ability of the male to find a mate. Stoneflies in general have high non-flight mobility (Hynes 1967) and flightless stoneflies may rely primarily on drumming (in many Northern Hemisphere species; Stewart 1997) or perhaps chemical attractants to facilitate the finding of mates.

Acknowledgments

I thank Mike Winterbourn for encouraging me to write this paper; Richard Purdon, Jo Ocock and Shannon Roughan for assistance in the field; and Bridget Allen for drawing the figures. Marek Kirs (Cawthron Institute) performed PCR extractions on larvae and adults to confirm identities of both. The Miss E.L. Hellaby Indigenous Grasslands Research Trust generously provided living expenses. Neil Andrews provided SEM images. I also acknowledge the late Ian McLellan who was the authority on this group and confirmed the validity of my description.

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Appendix 2

Namanereis tiriteae, New Zealand's freshwater polychaete: new distribution records and review of biology

This manuscript has been published as Gray, D.P.; Harding, J.S. & Winterbourn, M.J. (2009) *Namanereis tiriteae*, New Zealand's freshwater polychaete: new distribution records and review of biology. *New Zealand Natural Sciences* **34**: 29-38. Published formatting has been retained.

Abstract

A review of the biology of the poorly known freshwater polychaete *Namanereis tiriteae* is provided and new information on its distribution and habitat reported. *N. tiriteae* is now known from Wainisavulevu Creek, Fiji and four river systems (Manawatu, Tukituki, Ngaruroro, Waiapu) in the North Island, New Zealand. It has been found in open-canopied streams and rivers, including braided river channels and spring-fed, floodplain streams. Its habitats are typically a mixture of gravels, cobbles, sand and silt. Gut contents of individuals from a spring-fed stream were predominantly silt particles and diatoms, although a few arthropod fragments were also present. These observations suggest *N. tiriteae* may be a relatively indiscriminate deposit-feeder rather than an active predator as previously assumed.

Introduction

Most of the approximately 9000 species of bristle worms (Annelida: Polychaeta) are marine or estuarine organisms, although some 168 species in 70 genera and 24 families appear to be restricted to freshwater environments (Glasby & Timm 2008). They are widely distributed across the world but are most diverse in the Palaearctic region (67 species in 32 genera described from Europe, northern Asia and Africa) and least diverse in Australasia (31 species in 15 genera) (Glasby & Timm 2008). The best represented family, the Nereididae (Phyllodocida), includes 55 freshwater species, over half of which are in the subfamily Namanereinae (Greek, Nama, refers to a spring or stream). They include a single New Zealand species, *Namanereis tiriteae*, which was described from three specimens collected in the Tiritea (now Turitea) Stream near Palmerston North in 1968 (Winterbourn 1969).

Aspects of the biology and systematics of the genus *Namanereis* in the Caribbean region were reviewed by Williams (2004) who also provided a table summarising the distributions and habitats of 15 *Namanereis* species and species-groups. Seven of the nine Caribbean species have been found in springs and various subterranean habitats, as were several others including *Namanereis gesae*, a species found in Yemen (Fiege & Van Damme 2002) and not included in Williams' list. More recently, Glasby & Timm (2008) discussed the global diversity of all polychaetes in freshwater and touched on questions of their endemicity, phylogeny and zoogeography. A Gondwanan origin and radiation has been postulated for *Namanereis* (Figure 1) with a single colonisation of freshwater before the break up of Gondwana (Glasby & Timm 2008). Similarly, Haase *et al*. (2006) hypothesised a Gondwanan origin for the fresh-brackish water snail *Fluviopupa* (Hydrobiidae), although colonisation of Fiji, whose oldest islands are only about 40 million years old, must have been by long distance dispersal most likely from New Zealand or New Caledonia. A similar scenario may apply to *N. tiriteae*, but will require comprehensive phylogenetic analyses of the genus based on molecular data.

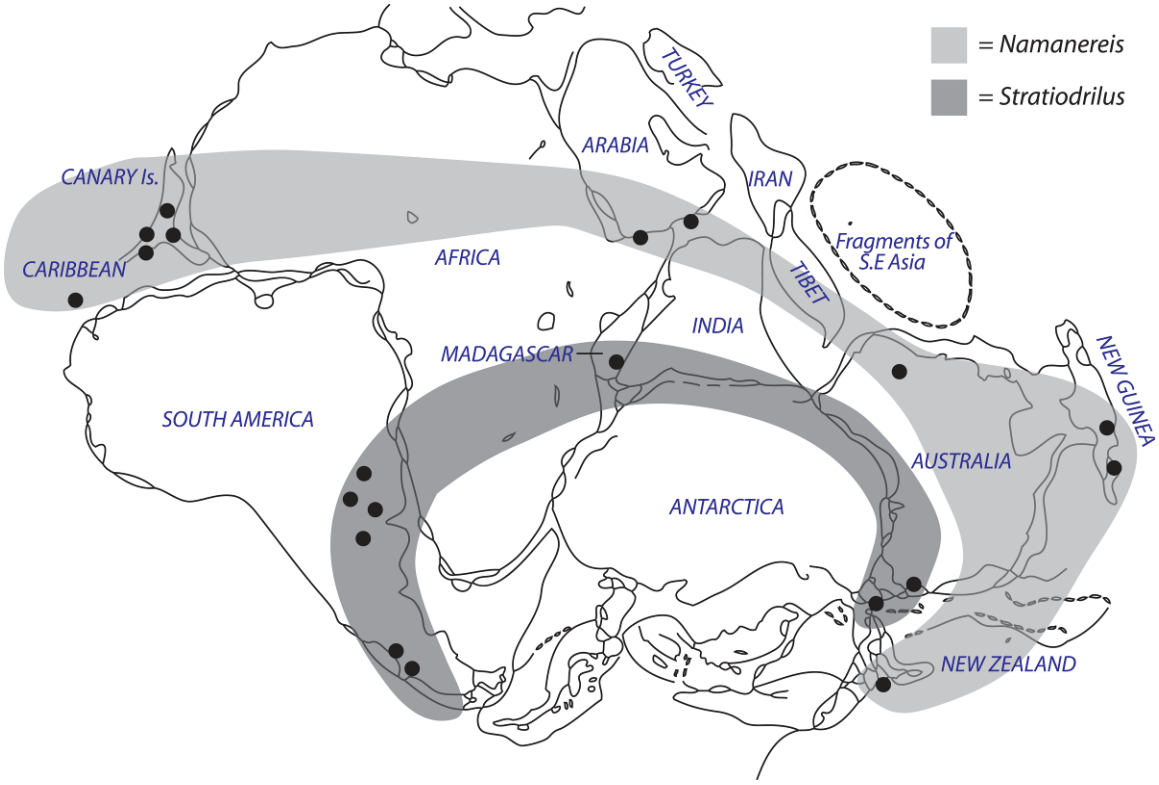

Figure 1. Distribution of species of *Namanereis* (Nereididae) and *Stratiodrilus* (Histriobdellidae) across Gondwana before its break-up in the mid to late Jurassic. Reproduced with kind permission of Chris Glasby.

The purpose of the present paper is to review knowledge of *N. tiriteae*, document new distributional records from the North Island and provide information on the habitats occupied by this elusive organism.

The New Zealand species of *Namanereis*

Two species of *Namanereis* are known from New Zealand, the euryhaline and morphologically variable *N. quadraticeps* (Blanchard) (regarded as a species group by Glasby 1999) and the freshwater species *N. tiriteae* (Winterbourn). The former is widely distributed in southern temperate and sub-antarctic regions, and in the New Zealand region specimens have been collected from brackish water and seawater pools on the Auckland and Campbell islands and from littoral clay banks on the Otago Peninsula, South Island (Winterbourn 1969). In contrast, *N. tiriteae* has been found only in inland rivers and streams; little is known of its biology (Scarsbrook *et al*. 2003).

Namanereis tiriteae

N. tiriteae was originally placed in *Namalycastis* Hartman based primarily on parapodial characters, although it was acknowledged at the time that it displayed features of both *Namalycastis* and *Namanereis* Chamberlin as then defined (Winterbourn 1969). Subsequently, Glasby (1999) transferred the New Zealand species to *Namanereis* and synonymised the Fijian freshwater species *Namalycastis vuwaensis* Ryan with it, stating that in terms of setal morphometrics the two groups of specimens were indistinguishable. All preserved New Zealand worms we have seen are unpigmented (white), although Ryan (1980) found that living specimens from Fiji were "a pronounced pink colour attributable to haemoglobin". In his original description of the species, Winterbourn (1969) also noted that the longitudinal blood vessels were prominent and red.

The largest of the three original specimens of *N. tiriteae* collected from Turitea Stream had a body length of 21 mm, whereas the holotype of *N. vuwaensis* from Fiji was 67 mm long. Recently collected material from Hawkes Bay and East Cape varied in body length and included the smallest recorded specimen (6 mm). Means and ranges of body lengths of intact individuals from three rivers are as follows: Tukituki River, mean 37 mm, range 21-52 mm, n = 15; Ngaruroro River, mean 9 mm, range 6-15 mm, n = 4; Waiapu River, 22 mm, n = 1. *Namanereis* species have giant-size ova and may have separate sexes or be hermaphroditic (Glasby 1999). However, we have found no individuals with eggs.

The head of *N. tiriteae* (Figure 2) bears a pair of antennae, prominent prostomial palps with hemispherical palpostyles, and three pairs of tentacular cirri. Eyes are absent. The eversible pharynx is armed with a pair of sclerotised, toothed jaws derived from the pharyngeal cuticle and formed by specialized epithelial cells called gnathoblasts (Tzetlin & Purschke 2005) (Figure 3). The jaws are "twisted about their long axis" (Ryan 1980) giving them a somewhat spoon-like form.

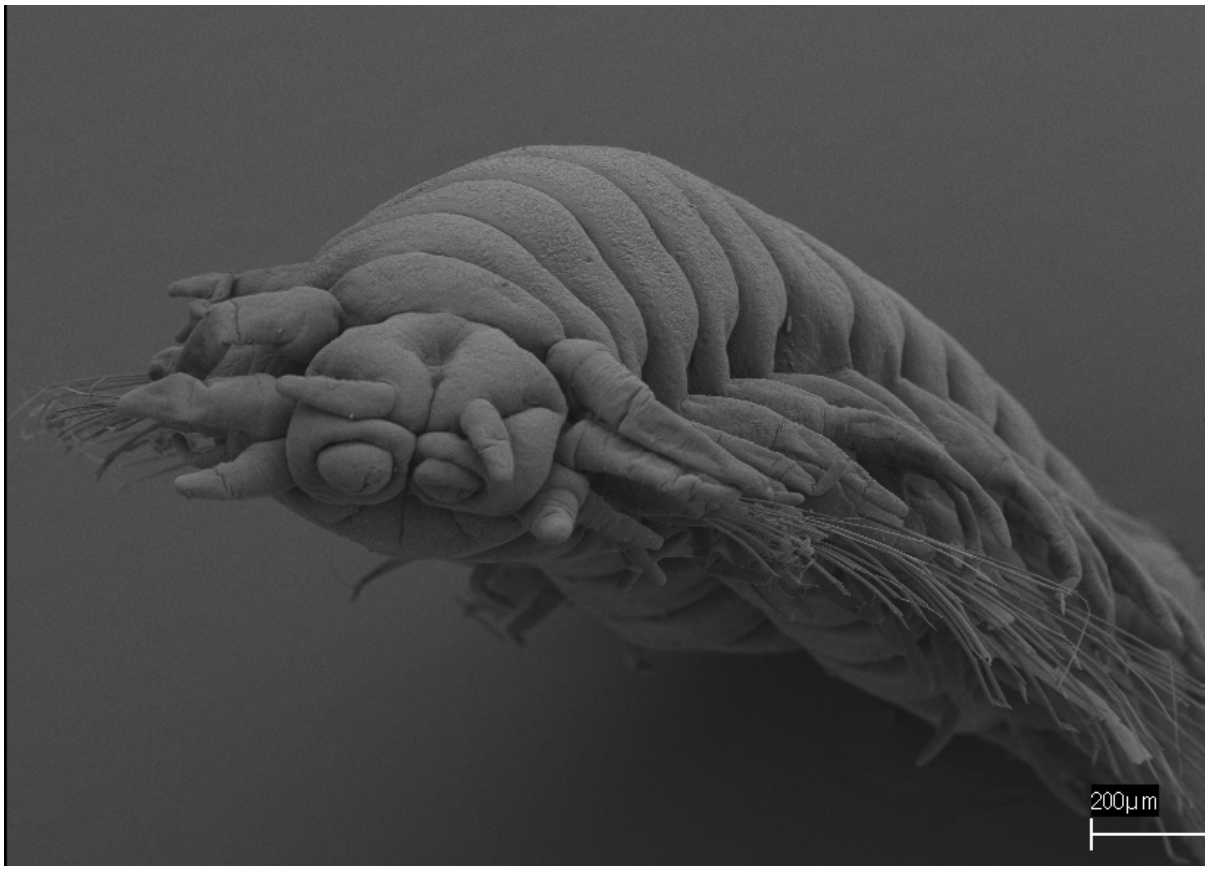

Figure 2. Scanning electron micrograph of *N. tiriteae* showing the head with antennae, prostomial palps, and three pairs of peristomial tentacular cirri. The parapodia of body segments have prominent setae and dorsal and ventral cirri.

In phyllodocid polychaetes such as Nereididae, jaw growth continues throughout life and is restricted to the basal region where growth lines may be seen (Figure 3c & d). New teeth are added at the base of the jaw as the worm grows (Tzetlin & Purschke 2005). Large individuals have up to 10 teeth (Figure 3e) and five were present in a 10 mm specimen (Figure 3a & b). Because the proximal, sub-terminal teeth are ensheathed, only the terminal teeth are visible on a scanning electron micrograph (Figure 3f).

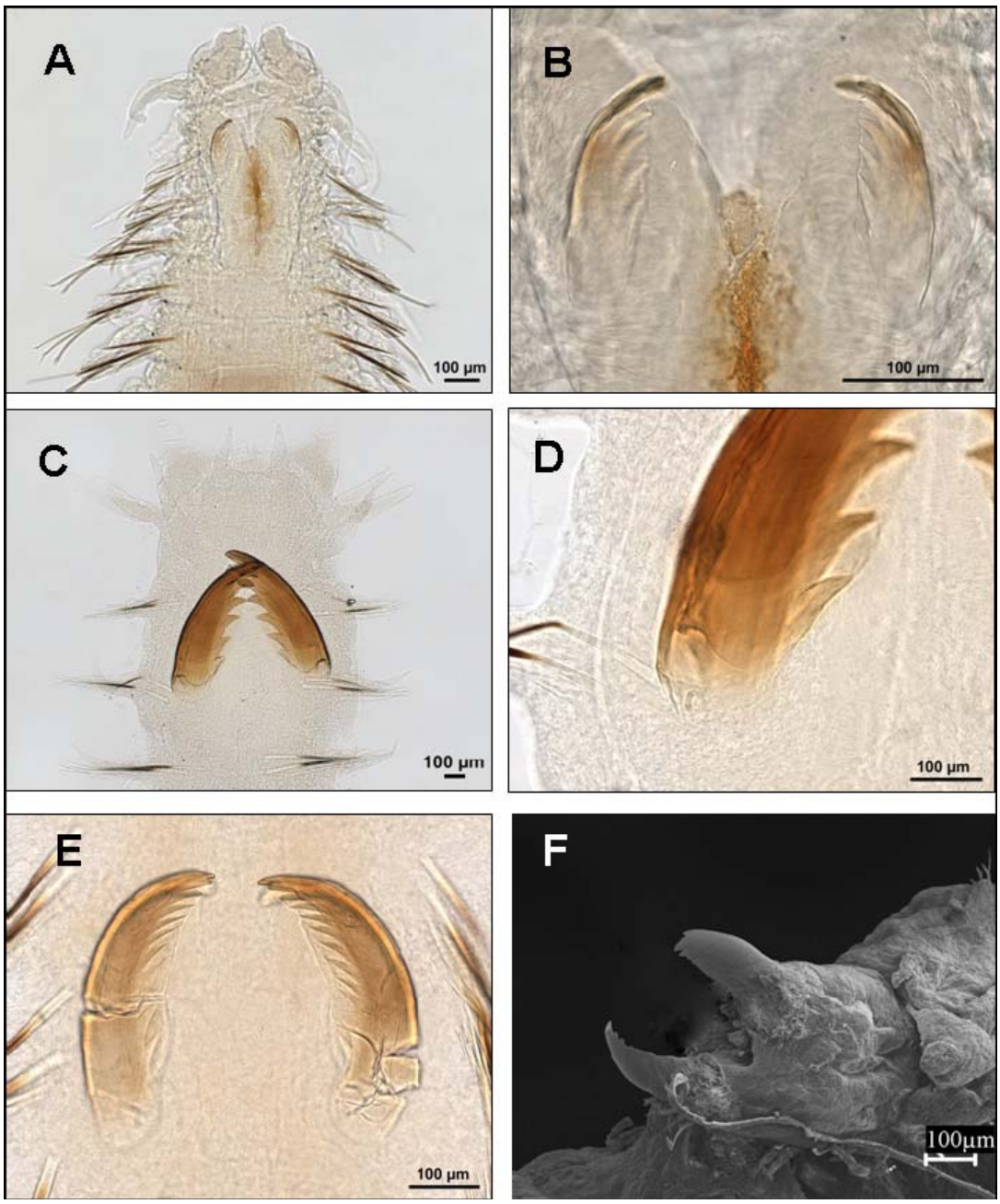

Figure 3. Light microscope images of the pharynx and jaws of *N. tiriteae*. A & B) dorsal view of head of a 10 mm long worm from the Ngaruroro River showing jaws with only 5 ensheathed proximal teeth and silt particles in the pharyngeal cavity; C & D) overview and basal growth lines in the jaw of a 50 mm long worm from Wainisavelevu Creek, Fiji collected by P. Ryan in 1974; E) jaws of a 40 mm long worm from the Tukituki River with at least 10 proximal teeth; F) scanning electron micrograph of the everted pharynx and jaws.

Distribution

All known distributional records for *N. tiriteae* are collated in Table 1 and its New Zealand distribution seems limited to several North Island rivers (Figure 4). In Fiji the species is known only from above the Vuwa Falls on Wainisavulevu Creek, Viti Levu, at least 100 km by river from the sea (Ryan 1980). At 700 m a.s.l. this is the highest altitude at which the species has been found.

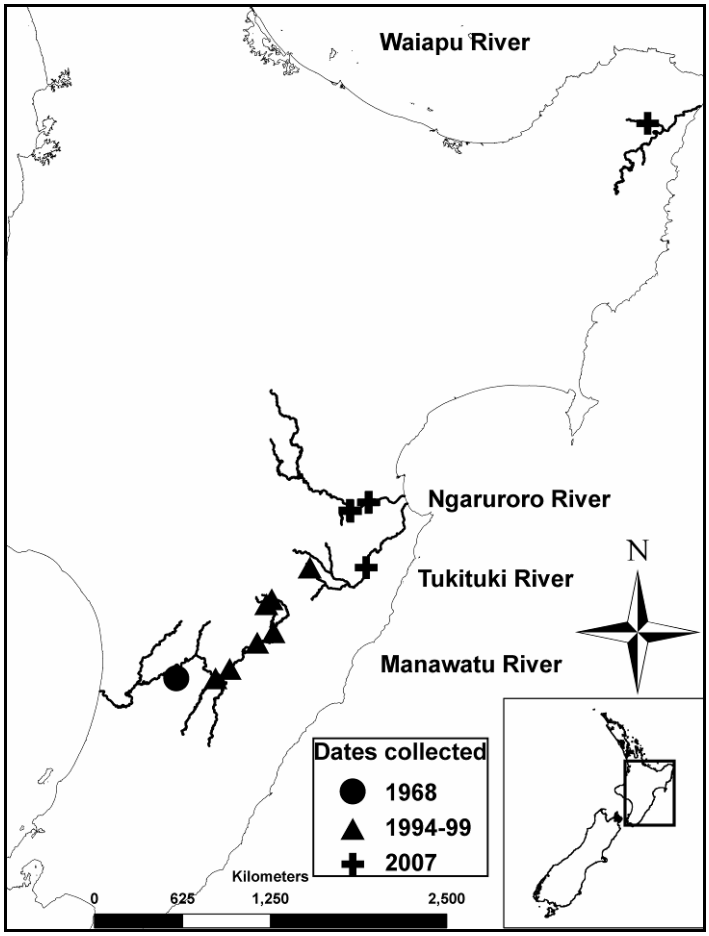

Figure 4. Locations of river systems and sites on North Island, New Zealand where *N. tiriteae* has been collected.

In New Zealand *N. tiriteae* has been found only in the North Island where its known distribution is restricted to four river systems (Figure 4). The original collection site, Tiritea (now Turitea) Stream, is a tributary of the Manawatu River. Subsequently, worms were found in other tributaries and the main stem of the Manawatu River and also the Tukituki River system in Hawkes Bay (Henderson 1995; Glasby 1999; McGuiness 2001). During a survey by one of us (DPG) in 2006-07 the known distribution was extended to

further sites in the Tukituki, the Ngaruroro River north of the Tukituki and the Waiapu River near Ruatoria, East Cape. Sites where *N. tiriteae* has been found are on 3rd to 6th order reaches of rivers and streams flowing through pastoral land. Channels were all weakly shaded and ranged in width from 1 – 21 metres (Table 2). Altitudes at which *N. tiriteae* has been found in New Zealand range from 40 to 406 m (Table 2).

Table 1. Locations, altitude and distance from the sea (river distance) of collection sites for *N. tiriteae* in North Island, New Zealand and Fiji.

Collection localities	Latitude South	Longitude East	Altitude (m a.s.l.)	Distance from sea (km)
D.P. Gray survey (2006-07)				
Tukituki River, Patangata Bridge	39˚ 53.31’	176˚ 43.40’	80	53
Ngaruroro River, above Fernhill Bridge	39˚ 35.97’	176˚ 43.34’	40	22
Ngaruroro River, Maraekakaho	39˚ 38.39’	176˚ 37.24’	80	34
Waiapu River, Waiorongomai	37˚ 51.95’	178˚ 11.34’	120	39
R. Fowler & I. Henderson (1994-2001 records; pers. comm.)				
Manawatu River, Hopelands Bridge	40˚ 21.70’	175˚ 57.64’	100	130
Manawatu River, Weber Rd	40˚ 14.37’	176˚ 06.84’	160	170
Manawatu River, Maunga Rd	40˚ 11.41’	176˚ 12.44’	200	190
Manawatu River, Ellison Rd	40˚ 02.72’	176˚ 11.36’	406	227
Mangatewainui River, Gundries Rd	40˚ 04.07’	176˚ 09.64’	383	213
Mangatainoka River, between Manawatu River confluence and Mangatainoka township	40˚ 24.18’	175˚ 52.89’	80	123
Manawatu River at Palmerston North	40° 22.40’	175° 36.87’	25	75
Ongaonga Stream, Ongaonga	39˚ 53.24’	176˚ 23.27’	220	100
Winterbourn (1969)				
Turitea Stream, Turitea	40˚ 24.91’	171˚ 39.71’	76	74
Ryan (1980)				
Wainisavulevu Creek, Viti Levu, Fiji	17˚ 49.92’	178˚ 02.50’	700	100+

N. tiriteae appears to have a strong affiliation for alluvial subterranean habitats and its distribution may be limited by the availability of such habitat. Thus, it is absent from river systems in the west and north of the North Island that do not exhibit the alluvial characteristics of those in the east. The apparent absence of *N. tiriteae* from large alluvial river systems in the South Island is a mystery but may be explained by the lower average annual temperature of subterranean waters. Summer water temperatures 6 metres below the surface in wells in Hawkes Bay (east coast North Island) and on the Canterbury Plains (eastern South Island) were 20.0 ^{o}C and 14.1 ^{o}C, respectively (Scarsbrook & Fenwick 2003). Water temperature may also influence the distribution of the stygobiontic isopod *Cruregens fontanus*, which has been found regularly in surface springs in the north but in deeper habitats such as wells and the hyporheic zone in the South Island (D. P. Gray unpublished data).

Habitat

Most worms have been collected in benthic samples taken from stony riffles dominated by gravels and in some instances sand. Most of the worms discovered in the 2006-07 survey were taken from a spring-fed creek on the Tukituki River floodplain (Figure 5), but others were collected from major braids, side braids and up-welling zones of the Tukituki, Ngaruroro and Waiapu rivers. Ninety percent of the individuals found in the study were associated with upwelling groundwater and in several instances the stygobiontic isopod *Cruregens fontanus* was present in the same samples. Although few individuals have been found at most sites, Reece Fowler (pers. comm.) took 116 worms from 42 benthic samples in the Manawatu River system, and 34 worms were taken in a single 0.1 m2 sample in a spring-fed creek on the Tukituki River floodplain (Gray unpublished data).

Table 2. Physico-chemical factors and benthic detritus biomass at sites where *N. tiriteae* was collected in the 2006-07 survey of braided rivers (n = 9).

Mean	Minimum		Maximum
pH	-	7.0	9.4
Conductivity (μS_{25} cm-1)	167	146	199
Temperature (^{o}C)	23	21	26
Dissolved oxygen (% saturation)	84	30	120
Max width (m)	6.6	1.0	21.0
Max depth (m)	0.24	0.04	0.70
Width/depth ratio	39	13	78
Max velocity cm s-^{1}	39	20	100
Substrate size (mm)	61	<1	420
Detritus (>1 mm) (g dry wt m-^{2})	2.81	0.39	11.11

Physico-chemical factors measured at sites in the 2006-07 survey are summarised in Table 2. Although streams and river channels varied considerably in size, they were generally shallow with a large width:depth ratio. Current velocities were also variable (range 20-100 cm s-1). Substrata were generally a mixture of cobbles, gravels and finer substrata but their relative proportions varied considerably among sites. No sites consisted solely of sand, silt or mud, but low concentrations of benthic detritus were typically present (Table 2). Most streams had circum-neutral to moderately alkaline pH and water temperatures greater than 21^{o}C, reflecting their lack of canopy cover and sampling in summer.

Figure 5. Spring creek in the Tukituki River bed, Hawkes Bay, where 34 *N. tiriteae* were found in a single Surber sample.

Although most specimens of *N. tiriteae* have been found within the top 5 or 10 cm of river beds, their lack of eyes and body pigment suggest that groundwater or the hyporheic zone may be more typical habitats (Henderson 1995, R. Fowler pers. comm.). According to Williams (2004) loss of eyes suggests a longtime association with subterranean habitats and springs, and all seven eyeless Caribbean species of *Namanereis* occur in these habitats. Nevertheless, despite extensive sampling of alluvial and karst aquifers throughout New Zealand, including aquifers alongside the Ngaruroro and Tukituki rivers, there have been no reports of *N. tiriteae* from groundwaters (M. R. Scarsbrook pers. comm.). However, Reece Fowler (pers. comm.) found three worms at a depth of 40 cm in hyporheic samples taken from the Ongaonga Stream, a tributary of the Tukituki River, and as already mentioned, 90 % of individuals collected in the 2006-07 survey were from up-welling reaches and therefore in contact with the hyporheic zone.

Food and feeding

Little is known about the feeding habits of namanereidid polychaetes, but it is usually assumed they are predatory (Williams 2004) or omnivorous (Glasby *et al*. 1990). The jaws of some phyllodocid polychaetes are used to capture and hold prey or to tear off pieces of algae and decaying matter, while those of some Eunicida are used for scraping food particles from hard substrates (Tzetlin & Purschke 2005). Like other species in the family, *N. tiriteae* has a muscular, eversible pharynx equipped with a pair of toothed, opposing jaws (Figure 3).

To determine what materials are ingested by worms we removed the gut contents from six individuals collected in a spring-fed stream on the Tukituki River floodplain. Most other worms appeared to have empty guts but the dissected individuals contained dark material that could be seen through the body wall.

Gut contents were mounted on slides in lactophenol-PVA and examined at up to 200 x magnification. Silt particles and diatoms were the most abundant materials found along with some fragments of filamentous algae, pollen grains and higher plant tissue. We also found a few arthropod fragments including claws, leg segments and sections of mayfly antennae. Ryan (1980) found chaetae of megascolecid oligochaetes in faecal material produced by *N. tiriteae* in Fiji and noted that oligochaetes were numerous in the polychaete's habitat. No oligochaete chaetae were seen on our slides, and few oligochaetes were found in the benthic samples that contained *N. tiriteae*. Instead the numerically dominant invertebrates were larval chironomids, mayflies (*Deleatidium*), tipulids (Eriopterini) and micro-caddisflies (*Oxyethira*). The most abundant "worm" taxon was the turbellarian *Cura pinguis*. It is possible that soft-bodied invertebrates, which are not visible in gut content analyses, were also eaten, or that the jaws are used to capture and dismember prey, and that only soft tissues and/or body fluids are actually ingested.

Stable carbon and nitrogen isotope analyses of various potential foods and prey species in the Tukituki spring stream were also made as described in Winterbourn (2007). All

material had been stored in ethanol for at least three months prior to analysis but this should have had little effect on the results (Kaehler & Pakhomov 2001; Sarakinos *et al*. 2002). Stable isotopes gave equivocal results (Figure 6), and did not help resolve the feeding question. Thus, although the stable carbon signature of *N. tiriteae* was similar to that of the predatory flatworm *Cura pinguis*, its nitrogen signature was almost identical to that of algae, lower than those of some primary consumers and higher than those of others. It is possible that *N. tiriteae* feeds relatively indiscriminately, and more in the manner of a deposit-feeding oligochaete than an active predator, as indicated by the predominance of silt and diatoms in guts. Additionally, the presence of silt in the pharynx in Figure 3a suggests that jaws may actually be used to shovel material into the buccal cavity.

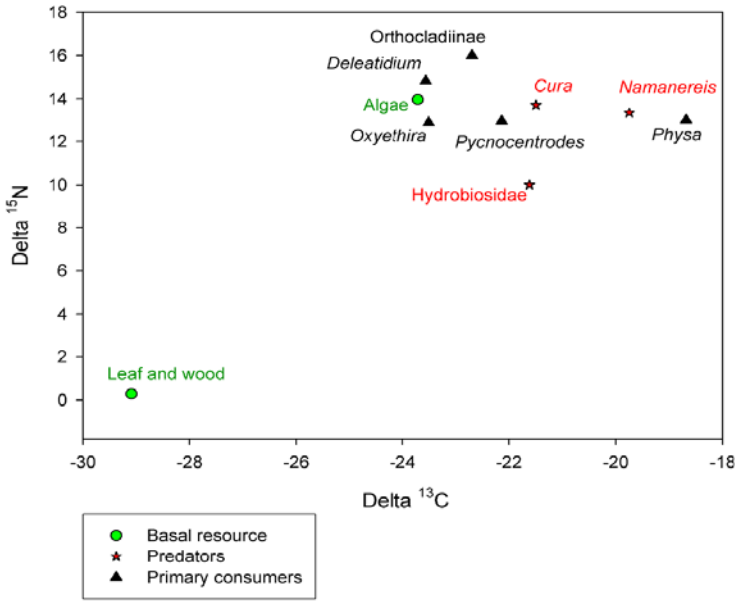

Figure 6. Stable isotope ratios of carbon and nitrogen from a spring creek in the Tukituki River, Hawkes Bay where 34 *N. tiriteae* were found. Material was stored in ethanol for 3 months prior to analysis.

Conservation and biodiversity

N. tiriteae is one of the least frequently encountered aquatic invertebrates in New Zealand. In 1995 Henderson published a request for further records of *N. tiriteae* in the newsletter of the New Zealand Limnological Society (now New Zealand Freshwater Sciences Society). However, after 12 years only two subsequent reports eventuated,

including this one (I. Henderson pers. comm.). Finding specimens of *N. tiriteae* at sites where they have been found previously has also been difficult, and no individuals have been found in either the Turitea Stream or Wainisavulevu Creek since the initial discoveries. Furthermore, although specimens have been collected intermittently at three sites in the Manawatu River catchment between 1994 and 2001, they have not been found subsequently in comparable numbers (I. Henderson pers. comm.). Collier (1992) listed *N. tiriteae* as a species of potential conservation interest and the few rivers in which it is known are in predominantly agricultural catchments susceptible to development, water abstraction and flood management. Clearly, further research is needed on this enigmatic member of our fauna to better understand its habitat requirements and population dynamics in order to enhance its conservation.

Acknowledgments

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Appendix 3. Presence/absence of invertebrate taxa in the eleven braided rivers included in our study.

	Waiapu	Ngaruroro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti
Ephemeroptera											
Ameletopsis	0	1	0	0	1	0	0	0	0	0	0
Atalophlebioides	1	1	1	0	1	0	1	0	1	0	0
Austroclima	0	0	0	1	0	0	0	0	0	0	1
Coloburiscus	0	1	1	1	1	0	0	0	1	0	1
Deleatidium	1	1	1	1	1	1	1	1	1	1	1
Ichthybotus	0	1	0	0	0	0	0	0	0	0	0
Mauiulus	0	0	0	1	1	0	0	0	0	0	0
Nesameletus austrinus	0	0	0	0	0	1	0	0	1	0	0
Nesameletus ornatus	0	1	1	1	1	1	1	1	0	1	1
Oniscigaster distans	0	0	0	1	1	0	0	0	0	0	1
Oniscigaster wakefieldi	0	0	0	1	0	0	0	0	0	0	1
Zephlebia	0	0	0	1	1	0	0	0	0	0	0
Neozephlebia scita	0	1	0	0	1	1	0	0	0	0	0
Plecoptera											
Austroperla cyrene	0	1	1	0	1	1	0	0	0	0	1
Cristaperla	0	1	0	0	0	0	0	1	1	0	0
Megaleptoperla diminuta	0	0	1	0	1	0	0	0	0	1	1

	Waiapu	Ngaruroro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti
Megaleptoperla grandis	0	1	0	0	1	0	1	0	0	0	1
Spaniocerca	0	1	0	1	1	0	1	0	1	1	0
Stenoperla prasina	0	1	0	0	1	0	1	0	0	0	1
Stenoperla maclellani	0	1	0	1	1	0	1	0	0	0	1
Taraperla howesi	0	0	0	0	0	0	1	0	0	0	0
Zelandobius	0	1	0	1	1	1	1	1	1	1	1
Zelandobius pilosus	0	0	0	1	1	0	1	1	1	0	1
Zelandoperla	0	1	1	1	1	1	1	1	1	1	1
Trichoptera											
Aoteapsyche	1	1	1	1	1	1	1	1	1	1	1
Beraeoptera roria	0	1	0	0	0	0	1	0	1	0	0
Costachorema psaropterum	0	0	0	1	1	0	0	0	1	0	1
Costachorema callistum	0	0	0	0	1	0	0	0	0	1	0
Costachorema xanthopterum	0	0	0	1	0	0	1	0	1	1	1
Edpercivalia	0	0	0	0	0	0	0	0	1	0	0
Ecnomina zealandica	0	0	0	0	0	0	0	0	0	0	1
Hudsonema alienum	0	0	0	1	1	1	0	1	0	1	1
Hudsonema amabile	0	1	1	1	1	1	0	1	1	1	1
Hydrobiosella	1	0	0	0	0	0	0	0	0	1	0
Hydrobiosis chalcodes	0	0	0	1	0	0	0	0	0	1	0
Hydrobiosis charadraea	1	1	1	1	1	1	1	1	0	1	0

	Waiapu	Ngaruroro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti
Hydrobiosis clavigera	1	0	0	1	1	0	0	0	0	1	1
Hydrobiosis copis	0	1	0	1	1	0	0	0	0	1	1
Hydrobiosis frater	0	0	0	0	0	0	0	1	1	1	0
Hydrobiosis harpidiosa	0	1	0	0	0	0	0	0	0	1	0
Hydrobiosis neadelphus	0	0	0	1	0	0	0	0	1	0	0
H. parumbripennis	1	1	1	1	1	1	1	1	1	1	1
Hydrobiosis silvicola gp	0	0	0	0	0	0	1	1	1	0	0
Hydrobiosis spatulata	0	0	0	1	1	1	0	1	0	0	0
Hydrobiosis soror	1	1	1	1	0	0	0	0	0	1	1
Hydrobiosis torrentis	0	0	0	0	1	0	1	0	0	0	0
Hydrobiosis umbripennis	1	1	1	1	1	1	1	1	1	1	1
Hydrochorema tenuicaudatum	1	1	1	1	1	0	0	1	1	0	1
Helicopsyche	0	0	1	1	1	1	1	0	0	0	0
Neurochorema confusum	0	1	0	1	0	0	0	0	0	0	0
Neurochorema	0	1	0	1	0	0	0	1	0	0	1
Oecetis unicolor	0	0	0	0	0	1	0	0	0	0	0
Oeconesus	0	1	0	1	1	0	1	0	0	1	0
Olinga feredayi	1	1	1	1	1	0	1	1	1	0	1
Oxyethira	1	1	1	1	1	1	1	1	1	1	1
Paroxyethira eatoni	0	1	1	1	1	1	1	1	1	1	1

	Waiapu	Ngaruroro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti
Paroxyethira hendersoni	0	1	1	1	0	1	1	1	0	1	1
Philorheithrus agilis	0	0	0	1	0	0	0	0	1	0	1
Plectrocnemia maclachlani	1	1	1	1	1	0	1	0	0	1	1
Polyplectropus	0	1	1	1	1	0	1	0	0	1	1
Psilochorema	1	1	1	1	1	1	1	1	1	1	1
Pycnocentria evecta	0	1	1	1	1	0	1	1	1	1	1
Pycnocentria funerea	0	1	0	1	0	0	1	0	1	1	0
Pycnocentrodes	0	1	1	1	1	1	1	1	1	1	1
Traillochorema	0	0	0	1	0	0	1	0	0	1	0
Tiphobiosis	0	0	0	0	0	0	0	0	1	0	0
Triplectides obsoletus	1	1	0	1	1	1	1	1	0	1	1
Triplectides cephalotes	0	1	0	0	0	0	0	0	0	0	0
Triplectidina	0	1	0	1	0	0	0	0	0	0	0
Coleoptera											
Antiporus femoralis	1	1	0	0	0	0	0	0	0	0	0
Antiporus strigosulus	1	1	1	1	1	1	0	1	1	0	1
Berosus	1	1	1	1	1	1	1	1	1	1	1
Elmidae	1	1	1	1	1	1	1	1	1	1	1
Enochrus	0	1	0	0	0	0	0	0	0	0	0
Huxelhydrus syntheticus	1	1	1	1	1	1	1	1	1	0	1
Hydraenidae	1	1	1	1	1	0	0	0	1	0	1

	Waiapu	Ngarururoro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti
Hyphydrus elegans	1	0	1	0	0	0	0	0	0	0	0
Hydrophilidae	1	1	1	0	0	0	0	0	0	1	0
Liodessus deflectus	1	1	1	1	1	0	0	0	1	1	0
Liodessus plicatus	1	1	1	1	1	1	1	1	1	1	0
Paracymus	1	1	0	0	0	0	0	0	0	0	0
Podaena	0	0	0	0	0	0	0	0	1	0	0
Ptilodactylidae	0	1	0	1	0	0	0	0	0	0	0
Rhantus suturalis	0	1	0	1	1	1	1	1	1	1	1
Staphylinidae	0	0	0	0	1	0	0	0	0	0	0
Scirtidae	1	1	1	1	1	1	1	1	1	1	0
Diptera											
Aphrophila	1	1	1	1	1	1	1	0	1	1	1
Austrosimulium	0	1	1	1	1	1	1	1	1	1	1
Ceratopogonidae	1	1	1	1	1	1	1	1	1	1	1
Corynocera	0	0	0	0	0	1	1	1	0	0	0
Chironominae	1	1	1	1	1	1	1	1	1	1	1
Culex	1	0	1	1	0	1	1	0	1	1	0
Diamesinae	1	1	1	1	1	1	1	0	1	1	1
Empididae	0	0	0	1	0	0	1	0	0	1	1
Ephydrella aquaria	0	0	1	1	1	0	1	0	0	0	0
Eriopterini	1	1	1	1	1	1	1	1	1	1	1
Hexatomini	1	1	1	1	1	1	0	1	1	1	1
Paralimnophila skusei	0	1	1	1	0	1	1	0	0	1	1
Limonia	0	1	0	1	1	0	1	1	1	1	0

	Waiapu	Ngarururoro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti
Molophilus	1	1	1	1	1	1	1	1	1	1	1
Muscidae	1	1	1	1	1	1	1	1	1	1	1
Neocurupira	0	0	0	0	1	1	1	1	1	1	1
Ochlerotatus antipodeus	0	0	0	0	0	0	1	0	0	0	0
Orthocladiinae	1	1	1	1	1	1	1	1	1	1	1
Paradixa	0	0	1	1	0	0	1	1	0	1	1
Pelecorhynchidae	0	1	0	0	0	0	1	1	0	0	0
Psychodidae	1	0	0	1	1	0	0	0	0	0	0
Neolimnia	0	1	0	0	0	0	0	0	1	1	1
Scatella	0	1	1	0	1	0	0	1	0	0	0
Stratiomyidae	1	1	0	1	1	1	0	1	0	1	0
Tabanidae	0	1	1	1	1	0	0	0	0	0	0
Tanyderidae	1	0	0	1	1	0	0	1	0	1	1
Tanypodinae	1	1	1	1	1	1	1	1	1	1	1
Zelandotipula	0	0	0	1	1	0	0	1	0	1	0
Mollusca											
Potamopyrgus	1	1	1	1	1	1	1	1	1	1	1
Gyraulus corinna	1	1	1	1	0	0	0	0	0	1	1
Haitia acuta	0	1	1	1	0	0	0	0	1	1	1
Austropeplea tomentosa	0	1	0	1	1	0	1	0	1	1	1
Crustacea											
Cruregens fontanus	0	1	1	0	0	0	0	0	0	0	0
Phreatogammarus	0	1	1	1	1	0	0	1	0	0	0

Waiapu	Ngarururoro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti	Waiapu
Paraleptamphopus caeruleus	0	0	0	0	0	0	0	0	0	0	1
Paracrangonyx	1	1	0	1	0	0	0	0	0	0	0
Paraleptamphopus subterraneus	1	1	1	1	1	1	1	1	1	1	1
Paratya curvirostris	0	1	1	0	0	1	0	0	0	0	0
Paracalliope fluvitalis	0	1	1	0	0	0	0	0	0	1	1
Others											
Namanereis tiriteae	1	1	1	0	0	0	0	0	0	0	0
Anisops wakefieldi	1	1	1	1	1	1	0	1	1	1	1
Copepoda	0	0	0	0	0	0	1	1	0	0	1
Archichauliodes diversus	0	1	1	1	1	0	0	0	0	0	1
Tricladida	1	1	1	1	0	0	1	1	1	1	1
Hirudinea	0	0	1	1	0	0	1	0	0	1	1
Microvelia macgregori	1	1	1	1	1	1	0	0	1	1	0
Nematomorpha	0	0	0	0	0	1	0	0	0	0	0
Oligochaeta	1	1	1	1	1	1	1	1	1	1	1
Ostracoda	1	1	1	1	0	0	1	1	1	1	1
Prorhynchus	0	0	0	0	0	0	0	0	0	1	0
Acari	1	0	1	1	0	0	1	0	1	1	1
Sigara	1	1	1	1	1	1	1	1	1	1	1
Hygraula nitens	0	1	1	1	0	1	0	0	0	1	1

	Waiapu	Ngaruroro	Tukituki	Wairau	Taramakau	Landsborough	Waimakariri	Rakaia	Rangitata	Waitaki	Oreti
Musculium novaezelandiae	0	1	1	1	0	1	1	1	0	1	1
Ischnura	1	0	0	0	0	0	0	0	0	0	0
Austrolestes colensonis	1	1	0	1	0	1	1	0	1	1	1
Xanthocnemis	1	1	1	1	1	1	1	1	0	1	1
Procordulia	0	1	0	1	1	1	0	0	0	1	1
Total	**56**	**95**	**72**	**99**	**83**	**58**	**72**	**61**	**68**	**81**	**82**